MEMOIRS

OF THE

California Academy of Sciences

Volume VII

Hydrographic History and Relict Fishes of the North-Central Great Basin

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CARL L. HUBBS, ROBERT RUSH MILLER, AND LAURA C. HUBBS

SAN FRANCISCO

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At the northeast end of this same range of mountains [Ruby Range], in the valley near the railroad town of Wells, are apparently bottomless fountains of water miles from any surface stream. It is but a few feet across the largest of them, the smaller could be crossed at a bound, and all are peopled with swarms of little fish, none of them over four inches in length. One hundred and seventy miles to the southwest are other wells in which can be found similar specimens of the finny tribe, but they exist nowhere else upon the continent. From what age, and condition of the past are they the relics?

From Thompson and West's History of the State of Nevada, 1881, edited by Myron Angel, page 18.

CONTENTS

HYDROGRAPHIC HISTORY AND RELICT FISHES OF THE NORTH-CENTRAL GREAT BASIN[1]

By

Carl L. Hubbs, Robert Rush Miller, and Laura C. Hubbs

INTRODUCTION

As a belated sequel to our summary treatise (Hubbs and Miller, 1948b) that correlated in general terms the hydrographic history and the remnant fish life of the Great Basin and other arid parts of western North America, we now report, with more intensive documentation, on a cluster of more or less completely enclosed (endorheic) basins in the center and very heartland of the Great Basin (tables 1, 2). This is a region wherein the geomorphic forces of the Basin and Range physiographic province have, during late Quaternary time, disrupted the topographic and drainage patterns to an almost unmatched degree. Here, bare remnants of fish fauna have survived in the extreme isolation that has resulted from the almost complete desiccation of an area that not more than a few thousand years ago was one-fifth covered by lakes fed by streams of ample flow.

The area selected for present treatment includes the contiguous drainage basins of 20 pluvial lakes in central and eastern Nevada and of one lake, slightly disjunct, in western Utah (fig. 1). To the northwest, north, and east, the 20 mostly separated basins in Nevada, are surrounded by the still largely integrated and much less fish-depleted Lahontan and Bonneville drainage basins. To the north, these two main drainage systems are narrowly conjoined, to separate the area being treated from the southernmost headwaters of the vast Columbia River system (the common divide between these drainages is reduced by a wedge of the Columbia River system to a straight-line distance of only 26 kilometers). On the south side, the selected depressions in Nevada adjoin basins that in pluvial time were parts of the Colorado River system or were separated therefrom by low sills. Beyond the southwest boundary lie the intensely arid, fishless "Area of Sterile Basins" and the basin of pluvial Lake Toiyabe (Hubbs and Miller, 1948b, pp. 45–51 and 44–45, respectively). Some endorheic basins have been somewhat arbitrarily excluded or included in our treatment, but we have maintained a set comprising, with a single exception, a contiguous area covering the north-central part of the Great Basin. This exception, that of pluvial Lake Pine (Wah Wah) in Utah, is wholly surrounded by the southwestern tributaries of the Bonneville system (p. 68).

Together, the basins of these 21 selected pluvial lakes well represent the many endorheic valleys of the Great Basin as a whole. The selected area is indeed one of great ecological and faunal stress. Next to the fishless "Area of Sterile Basins," it is characterized by the extreme disintegration of drainage systems and by the almost maximal depauperation of the fish fauna, accompanied by the extensive subspecific differentiation of the greatly isolated remnants of the fauna.

In this report we deal with the fishes as well as the hydrography of all 21 basins, with the exception that a detailed analysis of the fishes of the Lake Railroad system is reserved for later treatment. We have under preparation also an account of the Lake Alvord system, astride the Oregon-Nevada line, and its two fish species. The cyprinodont fishes of the Death Valley system have been analyzed in detail (Miller, 1948, 1961) and the paleohydrography of the region has

[1] Contribution from Scripps Institution of Oceanography, University of California, San Diego, and from the Museum of Zoology of The University of Michigan.

been treated (Miller, 1946; Morrison, 1965, fig. 5). The fishes of the Lahontan system were provisionally reviewed by Snyder (1917), but the field exploration of the fishes of the Bonneville system that he conducted in 1915 never led to a thorough treatment of the fauna. Still earlier, Snyder (1908) had dealt with the fish fauna of the Oregon lakes. These and other early studies call for revision, and the limited faunas of a considerable number of endorheic basins south, west, and northwest of the north-central Great Basin area herein dealt with remain in need of treatment, though a brief summary of the hydrography and of the fishes has been presented (Hubbs, 1941a; Hubbs and Miller, 1948b).

The studies that have been published on the basins of the West and on their fish faunas, and the investigations herein reported, have been limited very largely to field reconnaissance, to the questioning of local residents, especially early settlers, to studies of available maps, and to the conventional systematic examination of the preserved fish specimens. Much remains to be done along these lines, but other approaches need to be undertaken. Rewards may be anticipated from more intensive field studies of the basins, including precise levelling, from a thorough examination of the aerial photographs now available, and through research on the subsurface lacustrine deposits, to ascertain more securely the past drainage relations and the history of the ancient lakes. Similarly, more extensive and more reliable interpretation of the differentiating relict fishes of the sharply isolated remnant habitats may be expected through such emergent areas of research as electrophoresis, karyotype analysis (beyond the start we have made since 1969), breeding and transference experiments, and through population and behavior studies. Any evidence—now totally lacking—on Cenozoic fossil fishes in the area herein covered would be enlightening (p. 73).

As we have indicated a number of times, the Great Basin is a vast arena wherein there has long been an active interplay between the processes of faunal establishment and extinctions, habitat disruption, and the isolation and differentiation of the remnant fish population. Documentation of this interplay has been the key objective of this report.

An abstract of this study has been published by us (1970).

FIELD SURVEYS BY AUTHORS

The authors' acquaintance with the portion of the Great Basin herein under treatment dates from 1915 when the area was traversed by one of us (Hubbs, as student assistant to John Otterbein Snyder), en route by car to and from a summer survey of the Bonneville system. The recognition of some of the waters in the basins as isolated would have led to the initial collection of some of the fishes herein treated, had it not been for an emergency that forced return without delay.

Together, or separately, the authors carried on field work in the area and in related parts of the Great Basin in 1926, followed by major trips in 1934, 1938, and 1942, with briefer supplementary studies in various years from 1950 to the present.

Our field procedures included relentless questioning of informed local residents, including, by good fortune, a number of original settlers and their children, who aided greatly in orienting us at a time when mapping was crude and limited, in providing history on the rare flash floods of the desert region, in telling us which of the isolated waters and basins did or did not contain fish, and in clarifying which species were native and which were introduced. With such help we crossed and recrossed nearly all of the basins under discussion and various adjoining basins. We have felt rather confident that we have sampled nearly all of the springs or groups of springs containing native fish. Shoreline features of ancient lakes were diligently sought, and their altitudes were checked against possible outlet passes by use of Paulin precision altimeters. Other pertinent geographical and geological features were observed and recorded. An effort in 1938 to obtain data on the chemical

composition of the often highly mineralized waters of isolated springs unfortunately proved abortive (p. 95). Large samples of the native fishes were collected and carefully preserved, with extensive geographical and ecological notes. Through the years these specimens have been studied extensively, in comparison with material from various other Western waters. Many colleagues (pp. 244–246) have aided us with geological, ecological, and ichthyological data and advice.

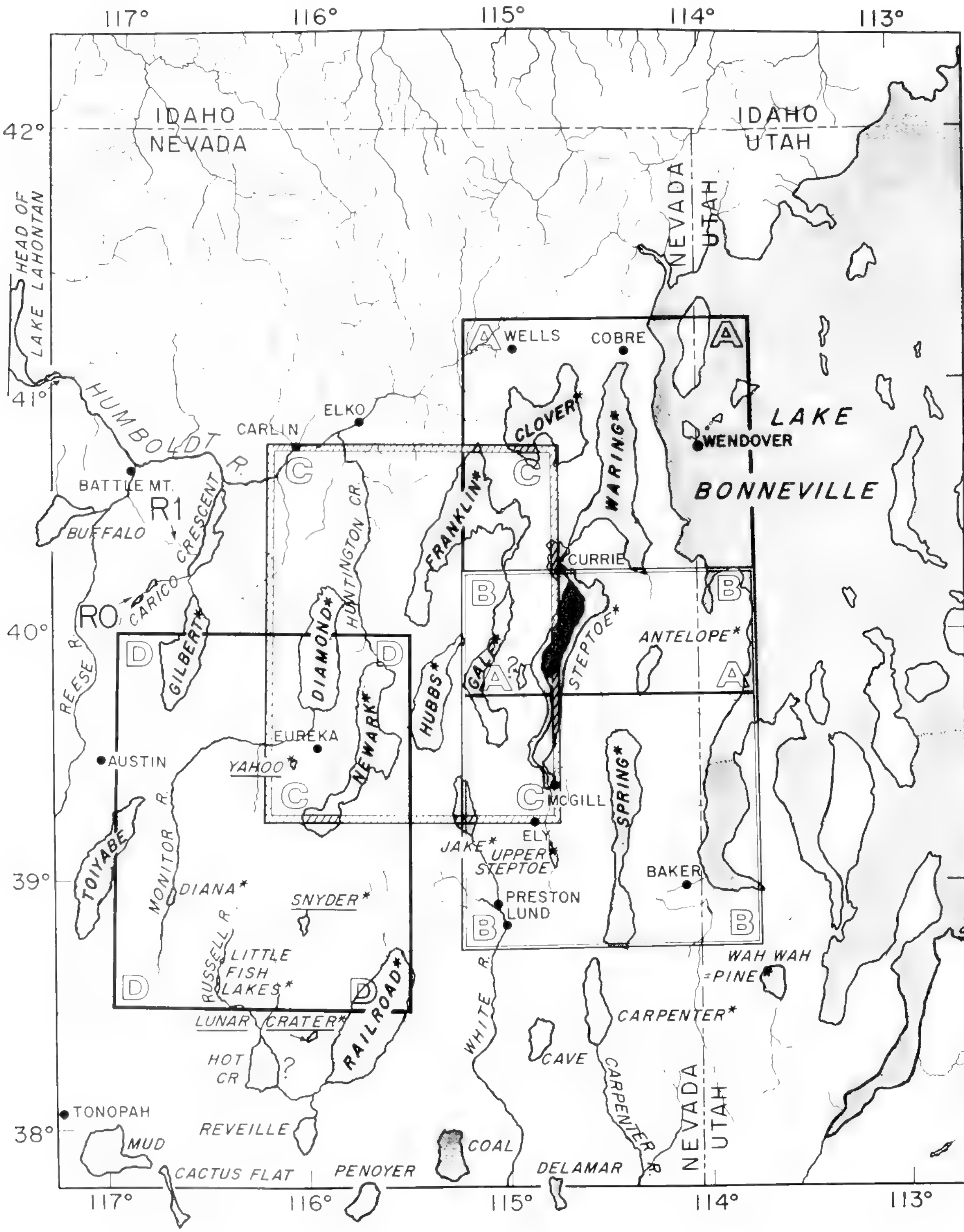
The preparation of this report, with help from many, has been underway since the end of 1964.

QUATERNARY PALEOHYDROGRAPHY OF BASINS IN THE NORTH-CENTRAL GREAT BASIN

The basins of the 21 selected pluvial lakes typify the many more or less disrupted fault-block depressions that feature the topography of the Basin and Range physiographic province, between the east-facing escarpment of the Sierra Nevada and the west-facing front of the Wasatch Range (Fenneman, 1931; Nolan, 1943; Blackwelder, 1948; Hubbs and Miller, 1948b; King, 1958; Snyder, Hardman, and Zdenek, 1964; Feth, 1964; Morrison, 1965). Most of these basins and the beds of their contained lakes are elongated in a more or less exactly north-south direction. They are bounded on one or both sides by great fault scarps, along which typically issue the valley-bottom or valley-edge springs in which, often almost unbelievably, a remnant of the fish life of the basin has somehow persisted. In contrast, the canyon and mountain-side springs of the basins, though seemingly permanent and hospitable, seldom contain native fish, presumably because occasional great flash floods, induced by the rare torrential precipitation of the desert region, sweep everything before them, then subside too rapidly to allow repopulation by return dispersal from the playa below.

Although many of the basins of the area have probably existed since at least late Miocene time, long enough to render plausible the retention of a few localized, trenchantly distinct, relict fishes (p. 70), most of the perceptible topographic and ichthyological evidence seems to pertain to post-Sangamon time, and much of it to the late Wisconsin. Most of the earlier physiographic evidence of ancient lakes and streams has been eroded away, and probably most of the fishes that earlier occupied the area have failed to survive. In our previous discussion (Hubbs and Miller, 1948b), we formalized the late events that are still signalized by ancient beachlines and other obvious physiographic evidence by referring to them, and to the lakes and streams that they represent, as Pluvial (with initial capital), but the suggestion has not been followed and we now abandon the practice.

We are also altering our former terminology in the naming of the pluvial lakes. Previously, we followed for most of these lakes the format of putting the name 'Lake' first, following the precedent of Lake Bonneville, Lake Lahontan, Lake Manly, Lake Algonquin, etc., but reversed the word order for certain basins when the combination seemed somewhat awkward or possibly confusing. Thus we used, among the lakes herein considered, Antelope Lake, Pine Lake, Railroad Lake, and Spring Lake. We now think it better to adopt the names Lake Antelope, Lake Pine, Lake Railroad, and Lake Spring, and the like, feeling that the consistent use of capital letters will preclude the double meaning. For ancient Upper Steptoe Lake we alter the word order to Upper Lake Steptoe. For the relatively insignificant ancient version of Little Fish Lakes we do not alter the word order.


117°
116°
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113°
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41°
40°
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IDAHO
NEVADA
IDAHO
UTAH
NEVADA
UTAH
HEAD OF LAKE LAHONTAN
HUMBOLDT R.
WELLS
COBRE
ELKO
CARLIN
BATTLE MT.
R1
RO
BUFFALO
CRESCENT
CARICO
GILBERT*
REESE R.
CLOVER*
WARING*
WENDOVER
LAKE
BONNEVILLE
FRANKLIN*
HUNTINGTON CR.
DIAMOND*
CURRIE
STEPTOE*
ANTELOPE*
GALE*
HUBBS*
NEWARK*
EUREKA
AUSTIN
YAHOO*
MONITOR R.
TOIYABE
McGILL
SPRING*
ELY
JAKE*
UPPER STEPTOE
BAKER
PRESTON
LUND
DIANA*
SNYDER*
RUSSELL R.
LITTLE FISH LAKES*
RAILROAD*
LUNAR
CRATER*
WAH WAH
=PINE*
CARPENTER*
WHITE R.
CAVE
CARPENTER R.
HOT CR
REVEILLE
TONOPAH
MUD
CACTUS FLAT
PENOYER
COAL
DELAMAR
A
B
C
D

The highest level and the discharges of some of the ancient lakes are indisputably demonstrated by beachlines and other evidence, but other connections remain more or less hypothetical (as is indicated in the detailed accounts that follow). In such cases, considerable weight has been given to the fish evidence, for the natural occurrence of the same or of very closely allied fish types is very strong evidence of a not very remote past water connection. Also, when clear evidence of beachlines is seen by field reconnaissance, or by the examination of the excellent topographic maps that have recently become available, to lie not far below the level of the assumed outlet pass, we venture the assumption that during occasional periods of unusually heavy precipitation the lake rose high enough to discharge. Anyone who has observed ordinarily dry playas of ancient lakes fill suddenly to a considerable depth by bursts of torrential precipitation, or to retain water for a considerable time in wet years, as in 1965, is not likely to doubt that during especially moist years such pluvial lakes overflowed at least briefly. Furthermore, the shoreline features of relatively early outlet levels and of temporary later ones may have been obliterated by time. We have relied on such reasoning to counterbalance the incomplete evidence for lake levels not quite high enough to insure discharge, particularly for lakes Gilbert (p. 11), Newark (p. 23), Carpenter (p. 65), and Jake (p. 67). For Lake Franklin (p. 42) and probably for Lake Clover (p. 30), at latest stages, we find indications of a subterranean discharge through alluvium.

In interpreting the hydrographic relations of the pluvial waters under consideration (tables 1, 2) and in their delineation (figs. 1–3, 7, 8, 11–14), we have relied largely on our earlier review (Hubbs and Miller, 1948b) and on the annotated map by Snyder *et al.* (1964), which was essentially copied by Feth (1961, 1964) and Morrison (1965, fig. 1), and, of course, on various earlier workers cited in these treatises. We have reviewed the field notes of our several reconnaissances, during most of which we used a precision Paulin altimeter. Our field trip in 1965 clarified the shoreline features of pluvial lakes Clover, Franklin, and Hubbs.

During recent years, even after the appearance of the new maps of Great Basin lakes just cited, a number of geologists have briefly treated these lakes, largely on the basis of the account and small-scale map by Flint (1957, pp. 226–233, fig. 13.2). Among these authors we cite Strahler (1963, pp. 357–358, fig. 31.25); Shelton (1966, pp. 352–363, figs. 331–343); Engel (1969, pp. 476–477, fig. 10); Longwell, Flint, and Sanders (1969, pp. 280–281, fig. 12.28); and Thornbury (1969, pp. 404–407, figs. 16.13, 16.14). Flint (1971, pp. 442–451, figs. 17.1–17.5) has further treated the lakes. A close approach to our present interpretations was issued by Morrison (1965, pp. 265–285, fig. 1), with a review of the depositional data, which were further treated by Morrison and Wright (1967).

←

FIGURE 1. Guide map to hydrographic features discussed in this report, and in adjacent areas; adapted from the map of Pleistocene lakes in the Great Basin, by Snyder, Hardman, and Zdenek (1964).

Indicated are areas, in clockwise sequence, D, C, A, B, as covered by the four pairs of detailed maps, respectively pluvial (figs. 2, 7, 11, 13) and modern (figs. 3, 8, 12, 14). Shown also are all recognized pluvial lakes in the area (named in sloping type, with new designations underlined); also many streams (major flows, and others helpful in showing drainage relations), and major towns. Stars designate the 21 pluvial lakes particularly treated in this report. The black center of Lake Steptoe represents the pluvial size that now seems to us most plausible. Otherwise, lake areas are essentially as mapped by Snyder *et al.*, generally in close agreement with us, except that we recognize, for a few lakes, somewhat hypothetical, higher maximum outlet levels (these outlets are depicted on this map, although the lake levels as charted would have been below spillage). Question marks denote two Pleistocene lakes that were recognized by Snyder *et al.* ('Hot Creek Lake' and one in Egan Valley on the western side of the Steptoe basin), but not accepted by us, at least as of pluvial age. R0 and R1 represent collections of *Rhinichthys osculus robustus*.

TABLE 1. *Basic data on the 21 pluvial lakes in north-central Great Basin treated in this report.*[1]

Pluvial lake name (alphabetical)[2]	Valley (for lake)	Area on fig. 1	Map: fig.	County (for lake)[3]	Discharged?[4]	Tributary to[4]
Antelope (29, 8[5])	Antelope	A, B	11, 13	White Pine	?	L. Waring (?)
Carpenter (66, 50)	Lake (Duck)	S of B	13 (N. end)	Lincoln, White Pine	Yes	Carpenter R. & Colorado R.
Clover (26, 15)	Clover, Independence	A, C	7, 11	Elko	Early[6]	Humboldt R. & L. Lahontan
Diamond (4, 68)	Diamond & Kobeh	C, D	2, 7	Eureka, Elko	Yes (early?)	Humboldt R. & L. Lahontan
Diana (—, 60)	Monitor	D	2	Nye	Yes	Monitor R. & L. Diamond
Franklin (24, 38)	Ruby & Butte (N)	A, C	7, 11	Elko, White Pine	?[6]	L. Clover (?)
Gale (25, 107)	Butte (S)	A, B, C	7, 11, 13	White Pine, Elko	Yes	L. Franklin
Gilbert (5, 70)	Grass	D	2	Lander, Eureka	Yes (early?)	Humboldt R. & L. Lahontan
Hubbs (31, 52)	Long	C	7	White Pine	Early??	L. Newark (??)
Jake (32, 45)	Jakes	B, C	7, 13	White Pine	Yes	White R. & Colorado R.
Little Fish (—, 51)	Little Fish V.	D	2	Nye	Yes	Russell R. & L. Railroad
Lunar Crater (—, 94)	Sand Spring	S of D	—	Nye	?	L. Railroad (?)
Newark (3, 64)	Newark	C, D	2, 7	White Pine, Eureka	Yes (early?)	Humboldt R. & L. Lahontan
Pine (Wah Wah) (1c, 88)	Pine	SE of B	—	Millard, Beaver (Utah)	No	Surrounded by Bonneville basin
Railroad (60, 80)	Railroad *et al.*	D + SE of D	2	Nye	Very early	White R. & Colorado R.
Snyder (—, 106)	(See text)	D	2	Nye	Probably	Lunar Crater L. & L. Railroad (?)
Spring (30, 98)	Spring	A, B	11, 13	White Pine	??	L. Bonneville (?) or L. Carpenter . . . Carpenter R. & Colorado R. (?)
Steptoe (27, 99)	Steptoe (north)	A, B, C	7, 11, 13	White Pine, Elko	Yes	L. Waring
Upper Steptoe (—, 100)	Steptoe (south)	B	13	White Pine	Yes	L. Steptoe
Waring (28, 38)	Goshute	A, B	11, 13	Elko	No	Nearest L. Bonneville
Yahoo (—, 81)	Yahoo	C, D	2, 7	Eureka	Yes?	Monitor R. & L. Diamond?

[1] Supplementary to table 2.
[2] The lakes constituting the block treated are marked with an asterisk on the guide map (fig. 1), to designate the area covered.
[3] All in central and eastern Nevada, except for Pine Lake, in Utah.
[4] At maximum lake level (in part somewhat hypothetical).
[5] The numbers in parentheses are, respectively, those used on the maps of Hubbs and Miller (1948b) and of Snyder *et al.* (1964).
[6] Discharge postulated as subterranean during late pluvial time.

Table 2. *Drainage relations, native fish species, depth, and areas of the 21 pluvial lakes treated.*[1]

Pluvial lakes[2] and drainage relations		Native fish species[3]	Est. max. depth, m.	Area of lake ÷ Area[4] of drainage basin	Total lake areas[4] ÷ Area[4] of entire basin
Lakes regarded as more or less disjunct from the Lahontan system					
Gilbert (5, 70)[5]		R	56 79	478 ÷ 1,528 = 31%[6] 565 ÷ 1,528 = 37%[6]	
Diamond complex	Diamond (4, 68)	G, R	45 76	792 ÷ 8,097[7] = 10%[6] 1,002 ÷ 8,097[7] = 12%[6]	811 ÷ 8,097 = 10%[6] 1,021 ÷ 8,097 = 13%[6]
	Diana (—, 60)	—	shallow	12 ÷ 1,339 = 1%	
	Yahoo (—, 81)	—	shallow	7 ÷ 44 = 16%	
Newark complex (?)	Newark (3, 64)	G	69 115	792 ÷ 3,587 = 22%[6] 1,146 ÷ 3,587 = 32%[6]	1,282 ÷ 5,264 = 24%[6] 1,636 ÷ 5,264 = 31%[6]
	Hubbs (31, 52)	—	63	490 ÷ 1,677 = 29%	
Clover (26, 15)		G, R	42	930 ÷ 2,624 = 35%	
Lakes regarded as having had early connections with both the Lahontan and Colorado systems					
Railroad complex	Railroad (60, 90A, B)	C, G	104	1,394 ÷ 10,874[8] = 13% 1,394 ÷ 12,343[9] = 11%	1,440 ÷ 12,343 = 12%
	Little Fish (—, 51)	G	shallow	11 ÷ 1,131 = 1%	
	Lunar Crater (—, 94)	—	shallow	11 ÷ 1,321 = 1%	
	Snyder (—, 106)	—	shallow	24 ÷ 148 = 16%	
Lakes containing the relict dace, in enclosed basins between the Lahontan and Bonneville systems					
Franklin complex	Franklin (24, 92)	S	53	1,314 ÷ 5,271[10] = 25%	1,788 ÷ 5,271 = 34%
	Gale (25, 10)	S	35	474 ÷ 1,933 = 25%	
Waring complex	Waring (28, 38)	S	66	1,314 ÷ 9,411[11] = 14%	1,734 ÷ 10,281 = 17%
	Steptoe (27, 99)	S	<30	282 ÷ 5,462[12] = 5%	
	Upper Steptoe (—, 100)	—	shallow	13 ÷ 816 = 2%	
	Antelope (29, 8)	—	23	125 ÷ 870 = 14%	
Lake separated by low divides from the Bonneville and Colorado systems					
	Spring (30, 98)	—	95	978 ÷ 4,337 = 23%	
Lakes regarded as having been tributary to the Colorado River system					
	Carpenter (66, 50)	—	<26	247 ÷ 1,257 = 20%	433 ÷ 2,371 = 18%[6] 496 ÷ 2,371 = 21%[6]
	Jake (32, 45)	—	33 46	186 ÷ 1,114 = 17%[6] 249 ÷ 1,114 = 22%[6]	
Lake enclosed within southwest corner of Bonneville system					
	Pine (Wah Wah) (1c, 88)	—	60	102 ÷ 1,912 = 5%	
				GRAND TOTALS	9,976 ÷ 54,028 = 18.5%[6] 10,690 ÷ 54,028 = 19.8%[6]

[1] Supplementary to table 1.

[2] The 21 pluvial lakes treated in this report are marked with an asterisk on the guide map (fig. 1), to designate the area covered; all may not have been strictly contemporaneous.

[3] C, *Crenichthys nevadae*; G, *Gila bicolor* subspecies; R, *Rhinichthys osculus* subspecies; S, *Relictus solitarius*.

[4] All areas given in square kilometers.

[5] The numbers in parentheses after the lake names are those used, respectively, by Hubbs and Miller (1948b) and by Snyder *et al.* (1964).

[6] For lakes Gilbert, Diamond, Newark, and Jake we give values for two estimates of the maximum level: first, one hardly subject to doubt; second, one based on the assumption of a discharge level, perhaps not attained during late pluvial time.

[7] Drainage area including basins of lakes Diana (evidence clear) and Yahoo (evidence unclear).

[8] Drainage area of Lake Railroad and the clearly tributary Little Fish Lakes, but not that of lakes Lunar Crater and Synder.

[9] Area including the dubiously tributary drainage basins of lakes Lunar Crater and Snyder.

[10] Including the certainly tributary drainage basin of Lake Gale.

[11] Including the certainly tributary drainage basins of Lake Steptoe and Upper Lake Steptoe.

[12] Including the certainly tributary drainage basin of Upper Lake Steptoe.

Of inestimable help have been the magnificently detailed and accurate topographic maps published in recent years by the United States Geological Survey (how these would have helped us in our earlier studies!). The entire area has been covered by 15 National Topographic Maps 1:250,000-scale located as follows, from north to south, in each of three vertical rows (from west to east), with dates of survey or of limited revision: (1) McDermitt 1959, Winnemucca 1958, Millett 1959, Tonopah 1959, and Goldfield 1958; (2) Wells 1958, Elko 1958, Ely 1959, Lund 1960, and Caliente 1959; (3) Brigham City 1958, Tooele 1958, Delta 1962, Richfield 1958, and Cedar City 1958.

The few then available earlier topographic maps, some on the 30-minute scale, were useful during the field work and still have some interpretive value. For historical purposes, as in tracing early explorations and original conditions, considerable use was made of old maps, including those in the reports of the Commissioner of the General Land Office for 1862 and, more particularly, for 1866 (see p. 233)—covering the early exploration of Nevada. Useful also, in the same connection, has been a copy of a map published during early years of mining entitled:

> Map of the States of California and Nevada, carefully compiled from the Latest Authentic Sources. By Chas. Drayton Gibbes, C. E. Comprising Information obtained from the U. S. Coast and Land Surveys, State Geological Surveys, by Prof. J. D. Whitney, Railroad Surveys, and the Results of Explorations Made by Brevet Lieut. Col. R. S. Williamson, U.S.A., Henry de Groot, C. D. Gibbes, and Others. Published by Warren Holt. 1873. No. 607 Clay Street. San Francisco, Cal. Scale 18 miles to one inch.

This map was indicated as having been drafted and lithographed by S. B. Linton, formerly of the U. S. Coast Survey. A much reduced copy was reproduced in the book by Wheeler (1971, opposite page 108). We have a photocopy of the original provided by the Bancroft Library. We have also checked the considerably detailed map of Nevada on pp. 830–831 of the Rand, McNally & Co.'s Indexed Atlas of the World, 1881 (in the senior author's library).

The paired modern and pluvial maps (reproduced as figs. 2, 3, 7, 8, 11–14) were sketched on and traced from these 1:250,000 maps, utilizing all evidence available to us. Where, as was true for a large share of the area, 15-minute topographic quadrangles had become available, the pertinent modern and ancient features were marked thereon and transferred to the 1:250,000 scale by a precise reducing apparatus. These 15-minute quadrangles were available for the entire area covered by 42 maps between 39° 00′ and 40° 45′ N. lat. and between 115° 30′ and 117° 00′ W. long., and for parts of the region east and southeast of those limits, for which the following sheets have been available (listed from north to south in 7 vertical rows, from west to east, the first row below the easternmost column of the main block): (1) Duckwater 1964, Blue Eagle Springs 1964, and Troy Canyon 1964; (2) Lamoille 1962, Illipah 1951, Treasure Hill 1949, Currant Mountain 1957, Currant 1964, and Forest Home 1964; (3) Riepetown 1959, Preston Reservoir 1959; (4) Spruce Mountain 1953, McGill 1958, and Ely 1958; (5) Spruce Mountain 4 1959, Schell Peaks 1959, Connors Pass 1959; (6) Sacramento Pass 1958, and Wheeler Peak 1948; (7) Garrison 1959 (see Index to Topographic Maps of Nevada). Within the Riepetown, Preston Reservoir, McGill, and Ely 15-minute quadrangles some 7.5-minute quadrangles have been available and have been used to check some features, particularly where in this area mining operations have obfuscated the topography. Here, an effort was made to portray the original condition. Use was also made, especially in our earlier work, of various other maps, including United States Geological Survey state maps, the United States General Land Office map of the State of Nevada (1930), United States Forest Service maps, and privately published county maps. Particularly helpful in the early field work was a map of White Pine County (Ed.

Millard & Son, Ely, 1930). Recently there has become available a vastly improved and very detailed United States Geological Survey map of the State of Nevada, 1:500,000 (compiled 1962, edition of 1965).

The topographic maps were especially valuable in tracing the divides between the various drainage basins, which were shown rather crudely on our 1948 map, drawn when very few such maps were available, and these fell far short of the high modern standards of cartography set by the new topographic maps. In this respect, even the map by Snyder *et al.* (1964) is somewhat generalized. The boundaries of the many drainage basins of the state have been delineated in fine detail on the map of State of Nevada Water Resources and Inter-basin Flows (Rush *et al.*, 1971), but on the basis of the modern rather than the pluvial drainage system.

The areas of the drainage basins were measured by planetary planimeter. The area in square kilometers (sq. km.) was determined after multiple measurements had been made of the areas in question and of 100 sq. km. on the 1:250,000 maps.

The pluvial lake margins were drawn largely by following a contour, or by interpolation between contours, on the most detailed topographic maps available, after points were fixed from field reconnaissance and map study and by comparison with the lake outlines as depicted by Snyder *et al.* (1964). In general, our conclusions agree closely with theirs. In utilizing contours, we have relied on the large mass of evidence that the ancient shoreline features have very seldom been considerably distorted during the geologically short time that has elapsed—about 10,000 to 30,000 years—since the still readily recognizable shoreline features were carved. In mapping the western shoreline of Lake Bonneville (figs. 11, 13), reliance was placed on new data on the isostatic deformation of the basin since the evaporation of that great inland sea (Crittenden, 1963).

Each of the 21 pluvial basins under treatment embraced a pluvial lake, ranging in area from about 7 to 1,394 sq. km., of which 10 (Gilbert, Diamond, Newark, Hubbs, Clover, Railroad, Franklin, Gale, Waring, Spring) covered at least approximately 500 sq. km. (table 2). Our two estimates for the total area of the 21 lakes, at maximum level, are 10,690 or 9,976 sq. km. (using two shoreline estimates for the area of lakes Gilbert, Diamond, Newark, and Jake): 19.8 or 18.5 percentage of the total estimated area (54,028 sq. km.) of the combined drainage area. Except for 6 very small and mostly stream-course lakes, listed as shallow, all of the 21 lakes are estimated to have reached depths between 23 and 115 m. (table 2). The total storage of surface water must have been immense—surely more than 100-fold greater than at present. The same can safely be said also of the differential in the proportion of the surface area that was covered by water. The two factors thought by some to have been adequate for the accumulation of surface waters during the Pleistocene, namely cooler temperatures and reduced evaporation, seem impotent, in themselves, to have produced the observed Pleistocene effect. For example, Cole (1968, p. 427) stated that ". . . . the existence of Pluvial lakes that are now ephemeral playas . . . . depended on lower mean temperatures, reduced evaporation, and the resultant increased runoff." With others, we feel that markedly increased precipitation must also have been involved—presumably in addition to and in correlation with these other factors. Snyder and Langbein (1962, p. 2394) thought it highly implausible that either an increase in precipitation or a decrease in evaporation could alone have caused the accumulation of Lake Spring; they stated: "the combination of an increase in precipitation from the present 12 to 20 inches [30–51 cm.] and a reduction in evaporation from 44 to 31 inches [112–79 cm.], that would restore Pleistocene Spring Lake, represents a most probable combination on a statistical basis." These estimates probably apply reasonably well to the north-central Great Basin as a whole.

The climatic basis for the accumulation of vast

bodies of water in the Great Basin has been expressed, consonant with our thinking, by a leading student of the Quaternary geology of the region (Morrison, 1965, p. 267) as follows:

> . . . . the Pleistocene climate fluctuated widely, with respect to both temperature and precipitation. The cooler and wetter times . . . called pluvials . . . . were . . . . 4.4° to 8.3° C cooler than now, and also appreciably less arid, as attested, for example, by markedly increased supply of coarse alluvium from the mountains and by increased mass-wasting. Runoff increased because of lower temperature and greater precipitation, tipping the balance between inflow and evaporation in the basins in favor of inflow, so that permanent lakes developed in all the terminal basins. These "lake cycles" or "lacustral intervals" were synchronous with intervals of glaciation in the higher mountains.

PLUVIAL LAKES REGARDED AS MORE OR LESS DISJUNCT FROM THE LAHONTAN SYSTEM

Seven of the 21 pluvial lakes under present study were in basins that are physiographically most closely tied to the Humboldt River division of the Lake Lahontan system, and most, perhaps all of these, were, we think, at some pluvial period actually within that drainage system. The four main lakes involved were Gilbert, Diamond, Newark, and Clover. Two very minor lakes, Diana certainly and Yahoo questionably, we associate with the Lake Diamond drainage system. The seventh lake of the series, Lake Hubbs, did not rise high enough, according to any definite evidence, to spill into Lake Newark.

Pluvial Lake Gilbert

Drainage basin on either side, near the middle, of the north-south line forming the boundary between Lander and Eureka counties (with the greater area in Lander County), in central Nevada (figs. 1, 2).

This rather large body of water was named pluvial Lake Gilbert by us (Hubbs and Miller, 1948b, pp. 35–36, 148, 157), "in memory of Grove Karl Gilbert's classical contributions to Great Basin hydrography." This name has been accepted by Snyder *et al.* (1964) and by Feth (1964). Lake Gilbert covered the large flat of Grass Valley and the lower levels of the adjoining bajadas. The middle of the valley toward the north end is occupied by a level, bare, sandy dry lake measuring 23 × ca. 3 km. on the Millett and Winnemucca 1:250,000 maps. The playa is rimmed, especially on the east side and around the north end, by sand dunes, some of considerable size. The south end of the valley, which is bordered on each side by high mountains, Toiyabe Range to the west and Simpson Park Mountains to the east, is less arid than the main part of the basin.

The drainage basin, that of Grass Valley (using this name, as is customary, to cover the whole basin, not merely the largely enclosed, more meadowy southern arm), is bounded as follows: at the north tip, in the immediate vicinity of the outlet, Cortez (Tenabo) Canyon, by the drainage basin of Crescent Valley, site of Lake Crescent (of uncertain age and status, for the valley maintains a flood-time outflow into Humboldt River—see p. 107); on the east side by the watersheds of Pine Creek, of the Humboldt River system, and by the drainage basins of Kobeh and Monitor valleys of the pluvial Lake Diamond system; on the south by the drainage basin of Big Smoky Valley, the site of pluvial Lake Toiyabe; on the west for a short distance by tributaries of Reese River, of the Humboldt River system, and for a greater distance by the watershed of Carico Lake Valley, which, like Crescent Valley, now is mapped as having a through drainage, but has been held to contain the bed of pluvial Lake Carico.

The drainage basin trends north-northeast to south-southwest. It is oblong, with a triangular tip at the northern, outlet end.

The basin measures 69 km. in greatest length and 32 km. in maximum width (at the north

end of the oblong area, most of which is about 25 km. wide). The lake was elongate, with a triangular expansion on the west side. We estimate its maximal length as 54 km. and its maximal width, at the submedian expansion, as 18 km.

We compute the area of pluvial Lake Gilbert at its assumed outlet level as 565 sq. km., approximating 37 percent of the area (1,528 sq. km.) of its watershed. The computations for the more completely authenticated, late Pleistocene lake level are: area 478 sq. km., 31 percent of the area of the watershed. At this lesser size (indicated by a dashed line on fig. 2) the primary dimensions would be 17 × 45 km.

Inasmuch as Lake Gilbert lay in the latitudinal belt of deep pluvial lakes, and as its rim rose to heights as great as 920 m., the great extent of this ancient lake and its probable attainment of an outlet are consistent with expectation.

The physiography and hydrography of this basin have been treated by Everett and Rush (1966) who mapped the lake below a discharge level.

Shoreline and Discharge.

Our reconnaissance of August 9, 1938, led us to believe that Lake Gilbert discharged northward into Crescent Valley, by way of a steep canyon, named Cortez or Tenabo. Above the dunes margining the dry lake, the bajada is marked on each side by terraces that cut transversely across draws and alluvial cones. As seen from Walti Hot Springs, on one of the lower terraces just east of the playa, a terrace on the west side seemed to line up with Cortez Pass, below which Cortez Canyon drops steeply into Crescent Valley. Altimeter readings indicated a succession of apparent beachlines from about 100 feet (ca. 30 m.) below to 100 feet higher than Walti Hot Springs. The uppermost terraces were rather faint, but seemed definite. A reading taken within an hour at the summit of Cortez Pass was only 10 feet (3 m.) higher. Near Cortez a broad saucer-like flat area, circling the north rim of the valley, is covered by seemingly lacustrine clay almost to the summit of the pass. It is assumed that at some pluvial time(s) Lake Gilbert spilled, but it does not appear to have long retained discharge during late pluvial time. The occurrence in the spring at Grass Valley Ranch of a very strongly modified form of the *Rhinichthys osculus* group (see below)is consistent with this view.

The depth of Lake Gilbert was estimated by Snyder *et al.* (1964) as 250 feet (76 m.). We attain estimates of 258 feet (79 m.) for the assumed outlet level and 183 feet (56 m.) for the more conservative and less questionable late Pleistocene level on the following bases. Several altitudes are given on the Cortez and Walti Hot Springs 15-minute quadrangles for the playa level as 5,617 feet (1,712 m.), and one is marked as "VABM" (Verified Altitude Bench Mark). The outlet level is taken as approximately 5,875 feet (1,791 m.) because the paired 5,900-foot (1,798-m.) contours run through the gentle pass and altitudes of 5,856 and 5,865 feet (1,785 and 1,788 m.) are given just above the 5,850-foot (1,783-m.) contours that cross the divide at the south and north sides. The less questionable and presumably later level is estimated, and mapped, as 5,800 feet (1,768 m.), because apparently clear evidence of lake terraces were noted as being 100 feet above Walti Hot Springs, which are mapped as issuing on the 5,680-foot (1,731-m.) contour (see cover photograph, Everett and Rush, 1966).

Both estimated lake borders (fig. 2) are mapped by utilizing the following 15-minute quadrangles: Cortez 1938, Hall Creek 1956, Walti Hot Springs 1956, Mount Callaghan 1956, and Ackerman Canyon 1956. These and the other available, pertinent quadrangles were used in delineating the divides that surround the basin.

The more profuse waters of possibly early pluvial times are indicated not only by high shoreline terraces and presumed discharge, but also by the strength and height of the stream terraces along the draws fanning into the southern end of Grass Valley. These terraces seem incompatible with the present stream flows, as do the

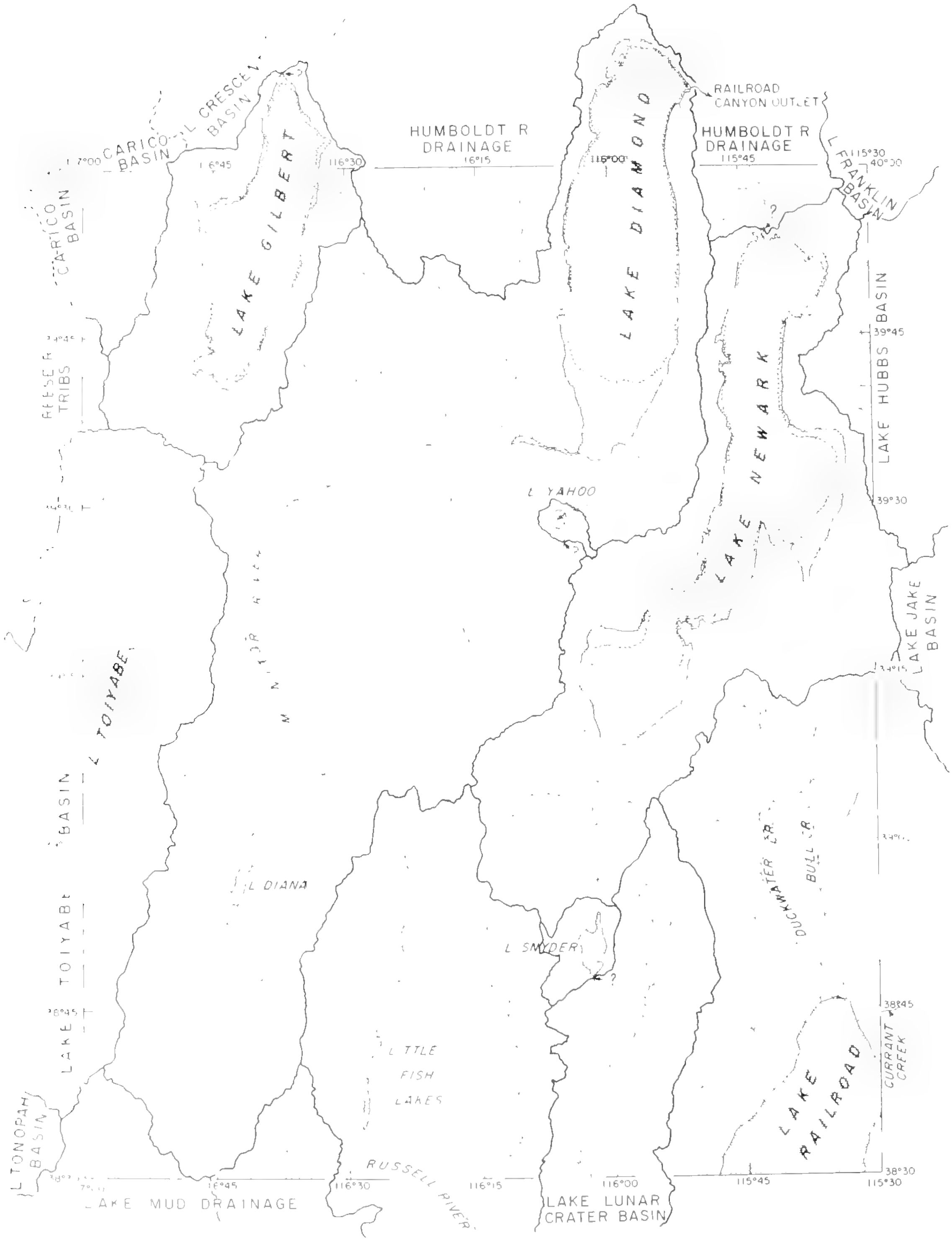


FIGURE 2. Detail of pluvial hydrography of southwestern part of study area ('D' on fig. 1).

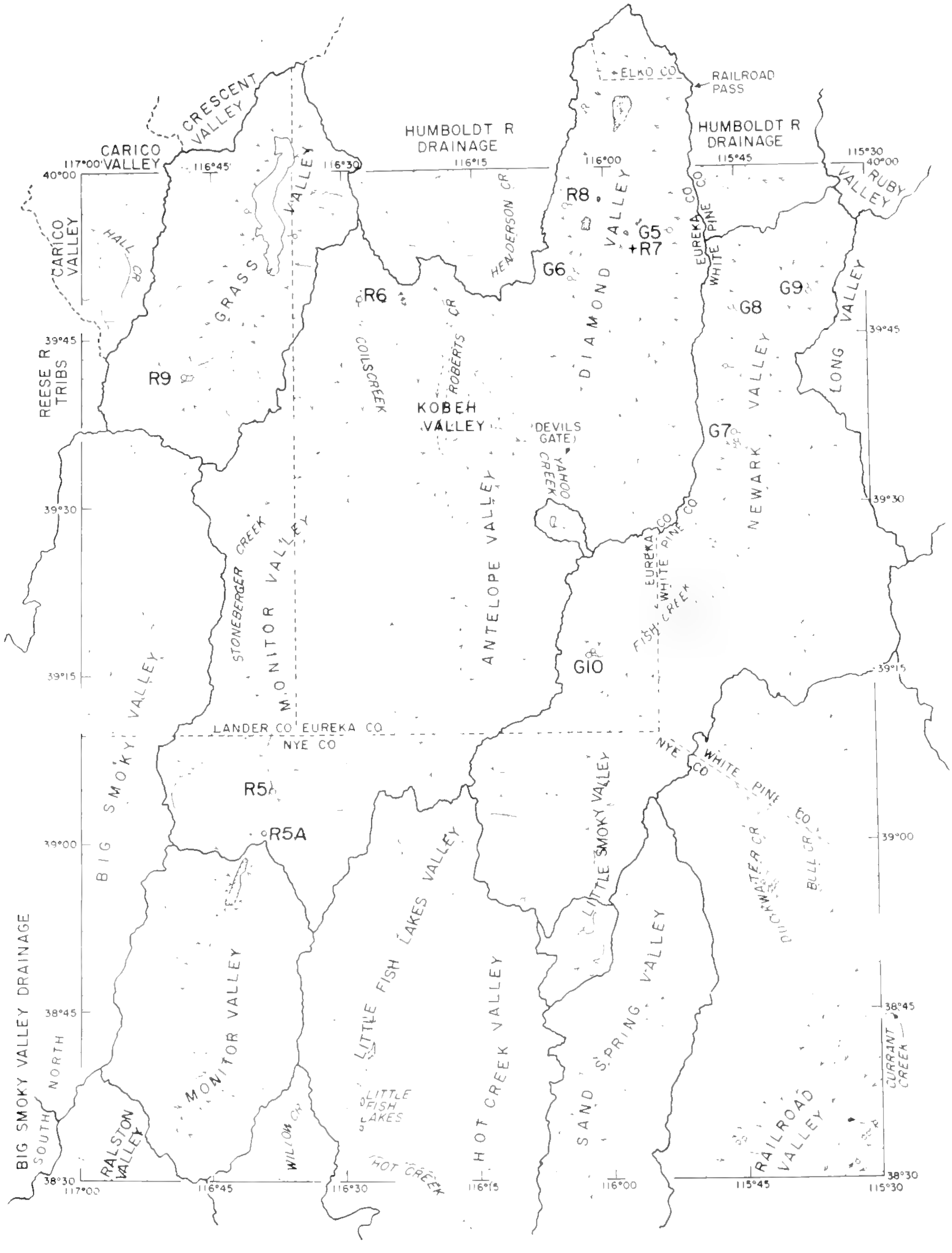


FIGURE 3. Detail of modern hydrography of southwestern part of study area ('D' on fig. 1); showing also key geographic features and Locations for *Gila* (G–) and *Rhinichthys* (R–).

terraces of the headwater stream courses (mentioned below) on the Big Smoky Valley side of the relatively gentle divide that separates that valley from Grass Valley.

Topographic evidence indicates that these headwater streams at the northern end of the drainage basin of Big Smoky Valley (fig. 3), within which the large pluvial Lake Toiyabe existed, flowed northward into Grass Valley prior to a natural diversion southward, probably in Pleistocene time. As we noted earlier (Hubbs and Miller, 1948b, p. 45), we found, northeast of Lake Ranch, what appears to be a stranded stream terrace that extends northeastward across the gentle divide between the present basins. Each of the two headwaters of the stream course in Rye Patch Canyon grades, at first northward toward a gentle pass into Grass Valley, just short of which each hooks backward in a hairpin turn to grade southward, so that flood waters discharge into the Toiyabe basin. One of the creeks at first flows northward and another, which heads near Box Springs, initially flows north and then northeast past Lake Ranch (see Mount Callaghan 15-minute quadrangle, 1956). A dry canyon on the north side of each divide appears to represent the former, now stranded, continuation of flow toward Grass Valley. The evidence is clearer on the east side, where no 40-foot contour crosses the pass between the stream (the outlet of Indian Ranch Spring) and the Grass Valley drainage, between the parallel 6,520- and 6,560-foot contours. On the west side, where the stranded terrace was observed, the southward diversion seems to have been much earlier, for the stream, where flowing northeastward beyond Lake Ranch, is rather deeply entrenched, and the north end of the valley has been even more downgraded, well below the pass altitude (between the 6,560- and 6,600-foot contours).

Remnant Waters and Fish Life.

Our local inquiries and field reconnaissance of August 9–10, 1938, led us to believe that the only waters in the Lake Gilbert system that retained native fish until modern time are those in the partly cut-off valley in which the headquarters of Grass Valley Ranch are located, west of the south end of the main depression. These waters, largely spring-fed, are in the lower valley of Callaghan (Woodward) Creek. This stream and its main, forked tributary, Skull Creek, rise on the east face of Mount Callaghan, which is assigned the altitude of 10,187 feet (3,105 m.) on the Mount Callaghan Quadrangle. We understand, from inquiries and from examination of the topographic map, that the flow from these streams is ditched, at times of adequate flow, onto the spring-fed marshes, for supplementary irrigation. When the fish sample (R9) was obtained, in 1938, a moderate quantity of water flowed, with slight to moderate current, through the wide wet meadow on Grass Valley Ranch, in Sec. 10, T. 21 N., R. 46 E. The creeks named above, along with Steiner Creek on the eastern side of the same arm in Grass Valley, are depicted as permanent on the available topographic maps (Mount Callaghan 15-minute and Millett 1:250,000), but we found the lower courses dry in August, 1938. We think it highly improbable that any of these canyon streams, or any in the main arm of Grass Valley, have retained native fish.

The only native fish that seems to have held out until modern times in this spring-fed meadow (or anywhere in the whole basin) is the strongly modified dace that we treat as a subspecies of *Rhinichthys osculus*, under the name of *R. o. reliquus* (pp. 121–128). In concordance with the hydrographic evidence, its distinctness seems to suggest not only its long habitation of a single spring area but also long isolation. The only other main valley springs in the basin, Walti Hot Springs, which lie on the valley floor east of the playa, in Sec. 33, T. 24 N., R. 48 E., were found to be far too hot for fish life. The streams that flow toward the valley from the higher mountains seem to be too impermanent and too subject to violent floods to have maintained fish since pluvial time. The apparent recent extinction of *R. o. reliquus* is discussed later (p. 123).

Whether fishes other than *Rhinichthys* occurred in the basin of Lake Gilbert in pluvial time is problematical. On the one hand, the steepness of Cortez Canyon (dropping about 265 m. in a straight-line distance of only 5 km.) suggests the possible exclusion of species not adaptable to swift water. However, the great difference in elevation of Grass and Crescent valleys may have been caused by tectonic movement since Lake Gilbert discharged. Furthermore, the occurrence of chubs of the subgenus *Siphateles* as well as of *Rhinichthys* in the basin of Lake Toiyabe (Hubbs and Miller, 1948b, p. 45) suggests that the establishment of those genera in the Toiyabe basin was most plausibly effected by a stream connection, discussed above, over the low pass from the basin of Lake Gilbert. The great differentiation of the *Rhinichthys osculus* in Grass Valley and the lesser modification of this species in Big Smoky Valley,[2] however, could be cited as inconsistent with this hypothesis, or as an indication of its early pluvial transfer into the Lake Toiyabe basin, followed by greater differentiation in the Lake Gilbert basin.

Pluvial Lake Diamond

Drainage basin in the extreme southwestern corner of the southern part of Elko County, over most of Eureka County, into the southeastern part of Lander County, and through the long Monitor Valley in Nye County, all in central Nevada (figs. 2, 7).

The large pluvial lake was named Diamond Lake by Hubbs (1941a, p. 65, fig. 4) and Lake Diamond by us (Hubbs and Miller, 1948b, pp. 34–35, 148, 157, figs. 10–12). This name has been accepted by Snyder *et al.* (1964) and Feth (1964). Its position essentially coincides with that of the large flat of Diamond Valley, with a southwestern tonguelike extension through the antecedent mountain gap known as Devils Gate.

[2] The *Rhinichthys* of Big Smoky Valley, as represented by material from Charnock Springs, has been described as a distinct species, *R. lariversi* (Lugaski, 1972), but our study of abundant material from this valley has led us to regard this local form as a rather weakly differentiated subspecies of *R. osculus*.

The drainage basin, much more extensive than Diamond Valley, is bounded on the north by the watershed of Humboldt River of the Lahontan system; on the east by the drainage basins of Humboldt River, and of lakes Newark and Railroad; on the southeast, south, and southwest by the "Area of Sterile Basins," as treated by us (Hubbs and Miller, 1948b, pp. 45–51); and on the west by the watersheds of Lake Toiyabe (not dealt with in this report) and Lake Gilbert (discussed above), and by the Pine Creek division of Humboldt River.

The Lake Diamond drainage basin comprises an elongate-elliptical, north-south oriented northeastern division, Diamond Valley, which contained almost all of the ancient lake at its highest levels and all of the lake during much of its history, and a larger drainage area to the west, through Kobeh Valley, and thence far southward. The basin in that direction comprises the large expanse of Monitor Valley, and, near the middle, also Antelope Valley, together with the intervening Antelope Range. The southwestern extension of the Lake Diamond drainage basin certainly embraces the watershed of Lake Diana, in Monitor Valley, and, doubtfully, that of Lake Yahoo, in the Fish Creek Range, between Diamond and Antelope valleys. Those two small lakes and their basins are separately treated below.

The entire drainage basin measures 208 km. in greatest length and, not far north of the middle, 85 km. in maximum width. The watershed of the Diamond Valley section extends 91 km. north to south and 33 km. west to east. Corresponding dimensions for the Monitor Valley section are 163 and 62 km.

We estimate that Lake Diamond at its highest (outlet) level was 70 km. in greatest straight-line length and 19 km. in maximum width. At the somewhat lower stand, which we have also mapped (as a dashed line), these dimensions were 55 × 18 km. We compute the maximum area of the lake as 1,002 sq. km., constituting 15 percent of the 6,758 sq. km. of the entire drainage

basin, including that of lakes Diana and Yahoo. At the lower level these figures are 792 sq. km., 12 percent of the basin.

Inasmuch as the altitude of most of the peripheral rim of the Lake Diamond drainage basin exceeds 2,500 m. and the basin lies in the latitudinal band of high pluvial precipitation and of high ratio between lake and drainage-basin area, it is surprising that the ratio for this lake is at most only 15 percent. This circumstance we interpret as corroborative evidence that the lake discharged, as we have indicated (Hubbs and Miller, 1948b, pp. 34–36, figs. 10–12).

With the exceptions certainly of Lake Diana, probably of Lake Yahoo, and possibly of Lake Snyder (see discussions below), no pluvial lakes can be postulated to have discharged into the drainage basin of Lake Diamond.

Deposits in the northern part of Kobeh Valley that were mapped by Merriam and Anderson (1942) as Quaternary, including lake beds, are too high to represent the western arm of Lake Diamond as we interpret it, but possibly represent the remains of a lake of some earlier period.

The ground waters of Diamond Valley have been described by Eakin (1962) who also mapped the shoreline of the ancient lake.

Shoreline and Discharge.

Reconnaissance determinations in 1938 of terrace elevations on the west side of Diamond Valley, toward the north, with the use of a Paulin altimeter, seem to confirm the idea that Lake Diamond discharged through Railroad Canyon. The altimeter readings seem to place the maximum altitude of the lake somewhat above the 6,000-foot (1,829-m.) contour as shown on the Winnemucca, Millett, Elko, and Ely 1:250,000 maps and on the 6 pertinent 15-minute quadrangles (Mineral Hill 1937, Railroad Pass 1959, Garden Valley 1959, Diamond Springs 1957, Whistler Mtn. 1956, Eureka 1953). Since the 6,000-foot contours are very closely approximated along Railroad Canyon, but do not conjoin there, it is concluded that the spillage downgraded the canyon and thus lowered the level of the lake while it continued to overflow. Weakness of terraces higher than the lip of the canyon seems to confirm this view. The present altitude of Railroad Pass is given on the Railroad Pass Quadrangle as 5,895 feet (1,797 m.). Since some of the lateral terraces were judged to be at an elevation of about 5,900 feet (see below), it is thought that the lake stood at about this height for some time. Our maps (figs. 2, 7) show lake borders at approximately 5,900 feet (1,798 m.), for the last outlet stage, as well as at about 6,000 feet (1,829 m.), to approximate the assumed initial outlet stage. Because the lake impinged against the steep west and east sides of the valley, these two lake levels are in general very closely approximated, except at the south end where the valley slope is very gentle.

The close approach of the same 6,000-foot contours through the inlet gap, Devils Gate, as well as in the outlet gap, Railroad Canyon, suggests that a tongue of the lake, at the highest level, extended westward through this trench slightly onto the broad desert flat beyond. According to the Whistler Mtn. 15-minute Quadrangle, checked by the planetable survey of 1956, the 6,020-foot (1,835-m.) interpolated contour extended 10.7 km. west of Devils Gate, in the mouth of Antelope Valley east of Lone Mountain. Assuming the outlet level at 6,015 feet (1,833 m.; see below), the tongue of the lake is estimated to have extended about 9.5 km. west of the Gate. The exact extent of the tongue is a bit uncertain, for the slightly earlier Millett 1:250,000 map shows the 6,000-foot contour extending 12.5 km. beyond the Gate, to a point southeast of Lone Mountain.

The deep trench at Devils Gate, west of Eureka, appears to be an antecedent water gap in the north-south file of mountains flanking Diamond Valley on the west, and the gap appears to date from some previous drainage system. It has obviously served, at all but the very highest stage of Lake Diamond, as the channel through which pluvial Monitor River flowed to reach Lake Dia-

mond. A figure in our former report (Hubbs and Miller, 1948b, fig. 12) made from a photograph, shows what may be a stream terrace on the south side just above the west end of this inlet pass.

On the west side near the north end of the lake, toward the south end of an island (or peninsula), a strong terrace (shown as fig. 10 of our 1948 report) was found to be close to the level of the outlet pass (Railroad Canyon), and traces of slightly higher shorelines were seen here. At Big Shipley Spring (Sadler Ranch, T. 24 N., R. 52 E.), altimeter readings taken rapidly and checked before and after against Bench Mark H 10 1936 (assigned elevation 5,836 feet), indicated the sharpest terrace at 6,020 feet (1,835 m.) and others at 5,915?, 5,965, 6,100?, and 6,075? feet. A second transect, taken farther south in the same township, midway between the Sadler and Bailey ranches, showed a broad terrace at about 5,895 feet (1,797 m.), well below the very strong terrace north of the middle of T. 23 N., R. 52 E., on the point just north of the Romano Ranch. That terrace was checked at 5,945 feet (1,812 m.) and a lesser terrace with the highest level of waterworn cobbles was tallied at 6,015 feet (1,833 m.). Several other terraces were traced, some well above the main outlet level, all around the north end, and on the faces of projecting points, which must have been exposed to waves, along the west side of the ancient lake. A sharp but rather low terrace rounds the point on the north side of the eastern end of Devils Gate, extending onto the desert flat, but this may have been a stream terrace. On the flat southeastern side of the basin, shorelines fade out, as is to be expected on such areas, where marsh vegetation no doubt inhibited shoreline erosion. Except locally, terraces are weak on the east side of the flat lake bed in Diamond Valley. Receding lake levels are suggested by dunes seen near the east edge of the alkali flat in the southern part of T. 25 N., R. 54 E. and by curved elevations shown on the topographic maps. These maps, however, show little in the way of shoreline features, presumably because the lake, during all but the latest stages of recession, impinged on the generally steep bajada. If the maximum altitude of the lake be regarded as 6,015 feet, and the altitude of the playa is taken as 5,767 feet, the depth of the lake above the playa level would have been 248 feet (76 m.). At the lower level mapped, the depth would have been 45 m.

Remnant Waters and Fish Life.

Diamond Valley. Most of the spring waters in the Lake Diamond drainage basin lie in Diamond Valley, which we reconnoitered in August, 1938. Here we found numerous spring waters, some profuse, mostly within but toward the edge of the flat shown on some maps as "Alkali Desert." These springs are more numerous on the western side of the valley, along the fault line at the base of the steep escarpment of the Sulphur Spring Range, than on the eastern side, along the foot of Diamond Mountain. We probably saw a sample of most of the springs on both sides. We treat the springs counterclockwise from the north:

"Lake Dou-pah-gate" was shown on the Land Office map of Nevada (1930) as much too large. This spring pool, in the northwest corner of T. 25 N., R. 53 E., was found to be only about 30 m. in diameter, very deep and chalky blue. It was reported to contain "bullheads" (presumably *Ictalurus* sp.), but no minnows. Careful observation around the edge and in the outlet slough and ditches disclosed no fish. This was probably one of two springs shown near Flynn Ranch on the Mineral Hill 15-minute Quadrangle, which also shows Josephine Spring one mile to the south.

Big Shipley Spring (of 1938), later mapped as Shipley Hot Spring, at Sadler Ranch (Location R8, figs. 3, 8), formed a large spring pond (fig. 21), or small lake, about 3 m. deep, of clear, warm, somewhat sulphurous water, with considerable vegetation. The cluster of head springs registered 39° C. The outlet was reported by a Biological Survey rodent-control agent then working in the area to extend about 5 miles (8 km.) onto the alkali flat, where some water accumu-

lates. The collection comprised goldfish and a local form, presumed to be native, of the speckled dace, *Rhinichthys osculus* (p. 115).

A spring just south of Big Shipley Spring was reported by the rodent-control agent to contain similar fish.

A rather large, very soft-bottomed spring hole in the yard of Bailey Ranch, in the southwest corner of Sec. 36, T. 24 N., R. 53 E., 3.2 km. south of Big Shipley Spring, was reported by the same informer to contain "chubs" and rainbow trout. Unfortunately we failed to check on this report, for the "chubs" may have represented a third population of *Gila bicolor* in the Lake Diamond drainage system. Or, this ranch-yard pool may have been stocked with chubs from Sulphur Spring or the Birch Ranch, for mosquito control or other reason.

Springs shown on the Garden Valley Quadrangle in T. 23 N., R. 52 E. between the Bailey and Romano ranches, at Romano Ranch, and for 3.2 km. farther south, the southernmost mapped as Tule Dam Spring, all obviously along the same fault line, were also not examined, but local testimony gave no indication that they contained fish.

Sulphur Spring (Location G6, figs. 3, 8), 14 km. by road south of Sadler Ranch, and now mapped as in Sec. 36, T. 23 N., R. 52 E. on the Garden Valley 15-minute Quadrangle, formed a partly artificial pool of clear water about 10 m. wide (described in some detail on page 154). It harbored a form that we interpret as a distinctive race of *Gila bicolor obesa* (Girard), one of the two we found in the whole drainage system. That this spring was probably long known to travellers is suggested by the long-used name of Sulphur Spring Mountain, that rims Diamond Valley on the west side.

The Garden Valley 15-minute Quadrangle shows a cluster of other springs within about 1 km. of Sulphur Spring. It is possible, though we think unlikely, that some of these springs and others mentioned above, all along the same fault line, may contain a remnant of native fish. There appear to be no prospects farther south on the west side of Diamond Valley, nor around the south rim.

A spring at Maggini Ranch, on the east side of the valley in Sec. 27, T. 23 N., R. 54 E., was found to be very small and fishless. The same almost surely applies to the two springs shown on the Diamond Springs Quadrangle in the same township between the Maggini and Thompson ranches. Close to one of these two ranches there is a small subterranean body of clear water known as Emerald Lake, in Emerald Lake Cave. Local claims of fish having been seen in this underground water have not been verified by Robert H. Soulages, biology student and active speleologist (personal communication, 1970), who will continue to look for fish here.

Two large springs on Birch Ranch (in 1938 the Jorge Jacobsen Ranch, later the Thompson Ranch), just off the base of Diamond Mountain, in Sec. 3 of the same township, yielded both *Rhinichthys osculus* (p. 115) and *Gila bicolor* (p. 154); mapped as Location G5 and R7 (figs. 3, 8). This is one of the two localities in all the basins under treatment that have retained both species. As noted later (p. 115), Mr. Jacobsen, who in 1938 had been on the ranch for 35 years, believed that the dace and chubs were native, and stated, in agreement with our findings, that fish occur on the east side of Diamond Valley only on his ranch.

These spring waters are apparently the southernmost of consequence on the east side of the great alkali flat. Proceeding northward we checked the ranches in an effort to locate other fish-inhabited waters (the narrow western slope of the Diamond Mountains offered no expectations). There were ranches at 1.4 and 10.6 km. along the almost straight road between Birch Ranch and Railroad Canyon, with no indication of sizable springs. Diamond Springs are named on the Diamond Springs Quadrangle at the site of the first ranch, and others are shown about a mile farther north. No springs were seen around the north end of the old lake bed, and none is shown there, save for a few small mountain springs, on

the Mineral Hill and Railroad Pass 15-minute quadrangles.

MONITOR VALLEY. Exploration and inquiries in 1938 led us to conclude that permanent surface water and fish, other than stocked trout, are confined to two spring areas, namely Coils Creek and Potts Ranch, in the wide expanse (see above) of Monitor Valley. Both areas were sampled. In 1972, fish were found in the discharge of hot springs about Dianas Punch Bowl, south of the Potts Ranch hot spring.

At the Three Bar Ranch on the course of Coils Creek (Location R6, fig. 3), near the north end of the basin (shown on the Roberts Creek 15-minute Quadrangle in Sec. 4, T. 22 N., R. 49 E.), a spring pool in grassy meadows yielded a large sample of one of the innumerable local forms of speckled dace, *Rhinichthys osculus* (p. 114).

In addition to Coils Creek, two mountain streams, Roberts and Ferguson creeks, are mapped as permanent, but each goes underground on a large alluvial bajada. We long thought that neither would seem likely to have retained fish. When examined on August 14, 1938, the stream at Roberts Creek Ranch was found to be very small, and it was locally reported to contain only stocked trout. However, one informant, biology student Robert H. Soulages (personal communication, 1970), has stated that he has seen small fish farther up Roberts Creek that he felt strongly were not trout. The locality is where the stream, near its forks, flows in a rather flat valley, as well as in a canyon (as shown in an aerial photograph supplied by Mr. Soulages). These fish may well have been speckled dace. Ferguson Creek was not examined, but the topographic maps raise little expectation that it contains native fish.

What we then thought to be Twin Springs on Bartine Ranch, on the flat area near the junction of Monitor, Antelope, and Kobeh valleys, were said by the rancher on August 15, 1938, to be of artesian origin and to contain no fish, and none were seen by us in the ditch and tank by the road. However, the Bartine Ranch 15-minute Quadrangle shows artesian wells at the ranch, and Twin Springs, Cold Spring, and Warm Spring, nearly 2 miles west, and other springs to north and south. Because springs in this location seemed to hold some chance of having retained native fish, those just named were checked by the Miller family on July 3, 1970. They were found to be of limited flow, without trace of fish, and to lack features associated with the retention of fish.

The other significant spring area in Monitor Valley for which we found evidence was at the hot springs (Locations R5 and R5A, fig. 3), near the south end of the axial stream course of the valley, now the largely dry southern branch of Stoneberger Creek.

One of the hot springs in this area was found on Potts Ranch (in Nye County, 9 km. south of Lander County), earlier known as Wilson Ranch. Here, clear water was found on August 16, 1938, to issue at 42° C. In the outflow, in a grassy meadow, where the water had cooled to 32–34 C., another local form of *Rhinichthys osculus robustus* (Rutter) was taken (p. 113). That the dace is endemic in this spring is indicated by the lack of any contrary evidence, by the rather copious water supply, by the location of the spring to one side of the main flood channel of the valley, and by the evidence of long continuity of spring flow furnished by the extensive travertine deposits beside which the water issues. The habitat and the fish population are described and discussed in some detail (p. 114, fig. 20).

During our reconnaissance in 1938, a local informant, a Forest Ranger named Crane, expressed the opinion, with which rancher George Potts agreed, that there is no reasonable chance that any fish other than stocked trout exist in any other waters of Monitor Valley (or in the valleys of Ralston and Stone Cabin creeks to the south). Nor did we find, through travel, inquiry, and examination of available maps, any other evidence of native fish life in Monitor Valley, or elsewhere in the entire western, intermittent drainage of Diamond Valley, except in the meadow area of Coils Creek and possibly in Roberts Creek (both discussed above).

Another hot spring issues, close to the course of pluvial Monitor River, in a meadow area of moderate size about 5 km. south-southwest of Hot Springs on Potts Ranch. This meadow was thought in 1938 to be fishless, but may have contained the ancestors of the fish found in 1972 in the hot-spring discharge discussed below. Farther on, 1.2 km. in the same direction, is another large, fishless hot spring known as Dianas Punch Bowl, which, strangely, forms a deep pool of clear water, which on August 16, 1938, was 7.5 m. in diameter, with a surface about 7 m. below the summit of a broad travertine dome measured by 1-foot altimeter as about 15 m. high (formerly the level was higher and now inactive holes on the sloping sides indicate former discharges).

Other hot springs (Location R5A) are shown on the Dianas Punch Bowl 15-minute Quadrangle (1960) as arising beside the road immediately southwest of Dianas Punch Bowl, and as forming the head of flow of the south branch of Stoneberger Creek. These springs we failed to see when the area was explored on August 16, 1938, and may well have then had a very limited discharge, in the meadow area that was then observed. However, in 1972 these springs yielded a stream flow for a short distance, in an apparently recently constructed ditch, and were found to contain a population of *Rhinichthys osculus* (Robert E. Brown, personal communication). The fish are in many respects like those of Potts Ranch Hot Springs, but sufficiently different in some details to suggest some degree of separation of habitat and of fish. In February, 1972, the main, westernmost of the springs in the ditch issued at 45° C. After it had turned northward the ditchlet percolated through a porous travertine deposit. Temperatures where fish were collected 100 m. above the barrier had cooled to 37.5°, and about 200 m. below the barrier to 37.0°. The flow below the barrier was about 0.3 cubic feet per second.

Slightly farther south, at approximately 39° 00′ N. lat., Box Springs, with a small fishless outflow, was found in 1938 to maintain a small meadow on the west face of an outlying hill of the Antelope Mountains. This lava hill, along with an alluvial cone from Mill Canyon (in the Toquima Range), dams the axial drainage of Monitor Valley to form an ephemeral lake, without outlet, the site of small pluvial Lake Diana (p. 21). At the time of our 1938 visit, this lake contained much water, following rains, but ordinarily it has no surface water and is of course fishless.

Except for the waters just described, in and near the course of ancient Monitor River, the surface waters of Monitor Valley are confined to very limited spring-fed sections in mountain canyons. Such habitats are almost always devoid of native fish life. Local testimony agreed with the expectation that no mountain streams in the valley are of sufficiently low gradient to have maintained native fish.

Evidence was also obtained in 1938 of the lack of native fish in the Antelope Valley arm of the southwestern part of the flood-water drainage system of Diamond Valley. Forest Ranger Crane and rancher Potts referred us to the rancher at Cerutti Ranch in Copenhagen Canyon in the Antelope Valley drainage for information on possible, though they thought improbable, native fish in Antelope Valley. That rancher was sure that no fish occur in the streamlet on his ranch (probably the one labelled Martin Ranch on Horse Heaven Mts. 15-minute Quadrangle), or elsewhere in Antelope Valley, wherein we saw none. We found Hot Spring in the same valley, shown on the Antelope Peak 15-minute Quadrangle in Sec. 28, T. 18 N., R. 50 E., to be too hot for fish. Although some streams are mapped as permanent in the adjacent mountains, we think it highly improbable that any native fish exist in the drainage system of Antelope Valley. We were intrigued with the name of "Fish Creek Well" in a canyon on the east side of the valley close to the probable course of the ancient outlet of Lake Yahoo, but the location seems most improbable for a native-fish habitat. Probably the well was named for Fish Creek Ranch and may have been drilled by Mr. Fenstermaker, the pioneer at that ranch across the Fish Creek Range. Fenstermaker

Wash, in Antelope Valley, is not far south of Fish Creek Well.

Pluvial Lake Diana

Drainage basin comprising the upper, southern part of Monitor Valley, near middle of north border of Nye County, central Nevada (fig. 2).

This very small lake, almost surely of pluvial origin and represented at present by the ephemeral lake discussed above, was named by Snyder *et al.* (1964). It was not discussed by us in our 1948 report, but was shown on our map of pluvial waters. In pluvial as well as modern time, as noted above, the lake appears to have been dammed by an alluvial cone, from the Toquima Mountains, impinging on a lava hill that juts into the valley from the Antelope Mountains.

The north margin of the drainage basin cuts across the Monitor Valley arm of the Lake Diamond watershed; to the east lies the Little Fish Lakes arm of the Lake Railroad system; to the southeast, south, and southwest occur tributaries of what we have called the "Area of Sterile Basins" (Hubbs and Miller, 1948b, pp. 45–51); and to the west, the drainage basin of Lake Toiyabe.

The roughly oval drainage is 58 km. in maximum (north-south) length and 31 km. in greatest width. Because of its position in the stream course down the axis of Monitor Valley, the pluvial lake presumably had, as Snyder *et al.* depicted it, approximately the form and dimensions of the present ephemeral lake, 9 km. long and 2 km. in greatest width (near the southern, inlet end). We estimate the area of Lake Diana as only 12 sq. km., 1 percent of the area (1,339 sq. km.) of the drainage basin.

Since this obviously integral part of the Lake Diamond hydrographic basin is bordered on each side by high mountains, mostly more than 2,700 m. in altitude, it presumably contributed much of the flowage in pluvial Monitor River, the main affluent to Lake Diamond. At present, its permanent waters are confined to the mountains and, we assume, are devoid of native fish life. We did find, however, as noted above, a population of speckled dace, *Rhinichthys osculus*, in the valley-spring water of Potts Ranch, and about Dianas Punch Bowl, which lies just below (north of) the location of Lake Diana.

Pluvial Lake Yahoo

Drainage basin in southeastern Eureka County, central Nevada (figs. 2, 7).

This lake was shown on our 1948 map, but was neither named nor discussed. It was mapped and indicated as a Pleistocene lake by Snyder *et al.* (1964) and by Morrison (1965, fig. 1), but was not named by them. Snyder *et al.* listed the valley as "Yahoo" but we note some discrepancy in the name. The modern remnant bears the noncommittal name Dry Lake on the General Land Office map (1930), and the Bellevue Peak 15-minute Quadrangle (1956) names Dry Lake Well along the margin of the playa. The name Yahoo was, we suppose, derived from the name of the canyon and creek that heads north beyond a low mountain ridge, although the apparent fault block basin opens southward into Spring Valley (tributary to Antelope Valley) along the course that we assume was taken by the ancient outlet of the lake. On the Millett 1:250,000 map the name given is Yahoe Creek, whereas the Whistler Mtn. 15-minute Quadrangle gives Yahoo Canyon. We suggest that the ancient lake be called Lake Yahoo, though it was of minimal size.

This minute drainage basin probably was included within, and certainly is entirely surrounded by the watershed of Lake Diamond (pp. 15–20), though it almost abuts on the Newark-Diamond divide. It is presumably a fault-block depression in the mountains, with the lowest pass, on the south side, above the 7,320-foot (2,231-m.), but below the 7,360-foot, contour (as shown on the Bellevue Peak 15-minute Quadrangle). As we have drawn the basin and lake borders after Snyder *et al.*, we measure the length and breadth of the basin as 12 and 6 km., and the length and

breadth of the pluvial lake as 3 and 2.5 km. We compute the area of the lake as 7 sq. km., constituting 16 percent of the area, 44 sq. km., of the drainage basin.

The topographic maps indicate that an intermittent playa pond exists within the old lake bed. Snyder *et al.*, on the basis of field work by Hardman, showed an outlet extending southward, then westward, to join the axial stream course of Antelope Valley, of the Lake Diamond system. We have no reason to question that conclusion, in view of the height of the surrounding mountains and the drainage relations of the adjacent basins.

We have not examined the basin, which we suppose has only intermittent surface water and no fish life.

Pluvial Lake Newark

Drainage basin in far-western White Pine County, the southeastern corner of Eureka County, and extreme northern Nye County, central Nevada (figs. 2, 7).

This lake, the main one in the area under treatment, was named and briefly discussed by us (Hubbs and Miller, 1948b, pp. 33–34). This designation has been accepted by Snyder *et al.* (1964), Feth (1964), and others.

The drainage basin is bounded on the north by Huntington Creek of the Humboldt River system (its inferred high-level outlet); on its northeast sector for only 6 km. (straight-line measurement) by a minor tributary of Lake Franklin; on the east mostly by the once possibly tributary basin of Lake Hubbs, and southward, for a straight-line distance of 16 km., by the Lake Jake watershed; on the southeast and south by the drainage basins of Lake Railroad and of Lake Lunar Crater and Lake Snyder, both perhaps tributary to Lake Railroad; and on the southwest and west, for about 15 km. each, by the Hot Creek and Little Fish Lake sections of the Lake Railroad basin; farther north on the west side, by the Lake Diamond hydrographic system.

The extensive area that drained in the pluvial period into Lake Newark comprised not only a northeastern part, Newark Valley proper, with a southern extension east of the Pancake Range, but also a southwestern arm, Fish Creek Valley, which is also commonly mapped as the northern part of Little Smoky Valley; the southern part of that arm is shown as extending not only across the southernmost part of the Newark drainage basin but also to and across the basin of pluvial Lake Snyder (pp. 37–38). Therefore, Fish Creek Valley seems to be regarded as a part of either Newark Valley or Little Smoky Valley. Even in historic time, Fish Creek Valley has drained occasionally into Newark Valley, but the valley is partly shut off from the Pancake Range by a mountainous prominence known as Black Point, which constricts the graben. Pancake Range separates the two southern extensions of the Newark drainage system.

Lake Newark occupied what is now an elongated playa, extending, as do the marginal mountains, north-south in Newark Valley and northeast-southwest in Little Smoky Valley and the connecting area. The extreme length of the total drainage basin is 132 km.; the greatest width, at middle, 55 km. The least width near the middle of the northern and southern parts, respectively, is 17 and 22 km. The lake area roughly conforms with that of the basin, but is displaced northward.

At the assumed outlet level the greatest straight-line length of the lake would have been 88 km. and the maximum width, in the southern part of the northern area, 20 km. The least widths, near the middle of the northern and southern sections, would have been 9 and 5 km., respectively; the greatest widths, toward the north and south ends, 14 and 17 km.

The area of the lake, at the discharge level, would have been 1,146 sq. km., or 32 percent of the area (3,587 sq. km.) of the drainage basin. When, if ever, Lake Hubbs discharged into Lake Newark (see p. 27), the drainage would have been increased to 5,264 sq. km. and the area of the lake would have constituted only 22 percent of the combined drainage area.

At the lower, unquestionable lake level shown on two of our maps (figs. 2, 7) as a dashed line, the lake dimensions would have been as follows: greatest straight-line length, 76 km.; maximum width, 18 km.; least width, north and south, 8 and 3 km.; area, 792 sq. km., or 22 percent of the drainage-basin area (exclusive of the Lake Hubbs basin).

The depth of Lake Newark above the level of the present alkali flat is estimated on the basis of the following numbers. The lowest assigned altitude of the alkali flat, which appears on the Buck Mountain, Cold Creek Ranch, and Eureka 15-minute quadrangles, is 5,833 feet (1,778 m.). The outlet-level contour as noted below is treated as slightly above the 6,200-foot contour and the lower level is treated as midway between the 6,040- and 6,080-foot contours. Assuming figures of 6,210 and 6,060 feet, the lake depths (above the present playa) are computed as 377 feet (115 m.) and 227 feet (69 m.). Snyder *et al.* gave an estimate of 285 feet (87 m.). The lower level we have drawn is probably over conservative. For example, as noted below, a definitive level just above Fish Creek Springs seems to be only about 45 m. below the outlet level. We regard the lower level drawn as uncontroversial and as representing a long-period steady state. This was the level accepted by Rush and Everett (1966, p. 10).

The large storage of water, on either lake-level assumption, is consistent not only with the position of the lake in the latitude of apparently heavy pluvial precipitation, but also with the height of the marginal mountains, especially the ranges on the abrupt west side (from north to south, the Diamond, Fish Creek, and Antelope ranges), which form a ridge almost uninterruptedly exceeding 2,500 m. in altitude.

The ground waters of Newark Valley have been described by Eakin (1960).

SHORELINE AND DISCHARGE.

There is a possibility that Lake Hubbs attained an early pluvial discharge into Lake Newark (p. 27) and a remote possibility that pluvial Lake Snyder overflowed into Newark Valley (p. 38).

That Lake Newark discharged into Huntington Creek and hence through Humboldt River into Lake Lahontan was claimed by us (Hubbs and Miller, 1948b, p. 33 and map). Our field notes (C.L.H.) of September 11, 1934, seem definite:

> Very clear wave-cut terraces were observed around the eastern side of Newark Valley. They were especially sharp and numerous around the north end of the valley, where they cut like steps into the evenly sloping valley sides. They reached just to the height of the ridge separating Newark Valley from Huntington Valley, indicating an outlet into the South Fork of Humboldt River.

Snyder *et al.*, on the contrary, stated that Lake Newark did not spill, and C. T. Snyder (personal communication) has indicated that he was not able to confirm such a discharge, either by field reconnaissance or by examination of aerial photographs, and that the shoreline he identified rounds the north end of the valley below the divide. Pending a more detailed survey, we maintain the view that Lake Newark did discharge during some pluvial, perhaps early pluvial, time. A prime basis for this assumption is our finding that the native fish of the Lake Newark basin, constituting in our judgment two local subspecies, are most closely related to *Gila bicolor obesa*, which is characteristic of the Lahontan hydrographic system. The degree of differentiation suggests a longer period of isolation than has befallen the Lake Diamond populations of *Gila bicolor* (and *Rhinichthys osculus*). We may have misjudged the height of the pass and may have interpreted a shoreline along an enclosed contour as being at the outlet level. However, shoreline features actually at the outlet level may well have become eroded beyond recognition during the probably long time since they were formed.

Our observations lead us to conclude that the highest outlet level of Lake Newark lay slightly above the 6,200-foot (1,890-m.) contour: at two points on the Cold Creek Ranch 15-minute Quadrangle, parallel 6,200-foot contours barely miss

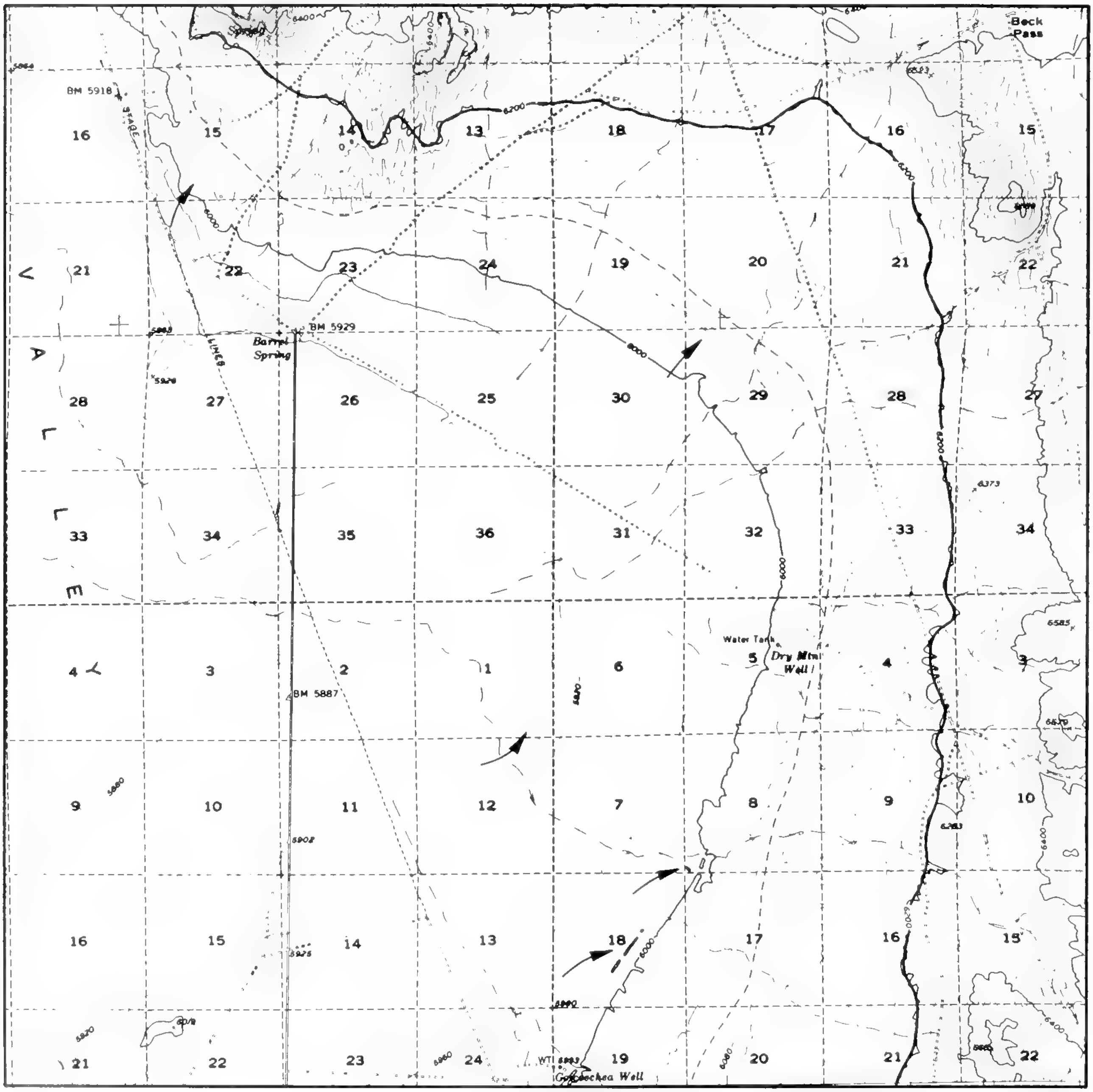


FIGURE 4. Shoreline features (bars and spits, pointed out by arrows) mapped along the 5,920-, 6,000-, and 6,040-foot (1,804-, 1,829-, and 1,841-m.) contours in the eastern embayment, near middle, of pluvial Lake Newark, western White Pine County, Nevada. These contours are 87, 167, and 207 feet (27, 51, and 73 m.) above the lowest stated altitude on the alkali flat of Newark Lake. Superimposed on a southeastern part of United States Geological Survey Buck Mountain Quadrangle (1957). Dashed line at 6,060-foot (1,847-m.) altitude is regarded as representing a minimal lake level, presumed to be late pluvial; heavy solid line at 6,200-foot (1,890-m.) altitude is regarded as an earlier-pluvial outlet level. Beck Pass in upper-right corner represents the possible early-pluvial outlet course of Lake Hubbs.

touching along the northern sill of the basin, where the drainage basin of Lake Newark contacts that of Huntington Valley of the Humboldt River watershed. We have, therefore, drawn the margin of the lake at maximum stage close to that contour on the Buck Mountain, Cockalorum Wash, Cold Creek Ranch, Diamond Springs, Eureka, Moody Peak, Pancake Summit, and Pinto Summit 15-minute quadrangles, and have had these transferred onto the 1:250,000 maps. In addition, we have drawn a second lake boundary, midway between the 6,040- and 6,080-foot (1,841-m. and 1,853-m.) contours, to represent a level clearly shown by the shoreline terraces seen and by strikingly bold longshore bars delineated along the 6,040-foot line in the eastern bulge near the middle of the lake, on the Buck Mountain 15-minute Quadrangle. This map also shows clear-cut recessional shoreline features (bars and spits) on the 6,000-foot (1,829-m.) and 5,920-foot (1,804 m.) contours (fig. 4). Dunes close to the 6,000-foot contour along the west side of a small flat just south of Fish Creek Springs (see below), at the foot of the bajada from Fish Creek Range, probably are also near an old shoreline of long standing.

Remnant Waters and Fish Life.

The most copious valley waters in the Newark drainage basin consist of Fish Creek and its headwater springs on Fish Creek Ranch in Fish Creek (Little Smoky) Valley, and several springs margining the flat bed of Newark Valley.

The profuse Fish Creek Springs (Rush and Everett, 1966, pp. 14, 25, 29), the sole habitat of *Gila bicolor euchila* (pp. 168–169), rise on the old lake bed near the western edge of its south-end expansion, about 5 km. west of Fish Creek Ranch headquarters, in the NW. ¼ Sec. 8, T. 16 N., R. 53 E. (as is shown on the Bellevue Peak and Pinto Summit 15-minute quadrangles). In 1938 there was one main spring north of two in tandem, with outlets soon joining in a meadow to form Fish Creek above the ranch headquarters. The more recent topographic maps show the spring source extensively draining into irrigation ditches. The spring water may originally have maintained Fish Creek for a considerable distance, but by 1938 or earlier it was usually consumed on Fish Creek Ranch, and was dry at the road crossing 7 km. below (east of) the springs on August 17, 1938 (well after the 1934 drought). Isador Sara, the Basque who had long operated Fish Creek Ranch, testified when interviewed on that date, that about 25 years previously water from Fish Creek reached Newark Valley. It did so when he ditched the creek on the valley flat in an effort to irrigate some lower fields (in the winter this was done to prevent the freezing of the fields). As a result, wagons mired along the old road. Ordinarily, he said (as of 1938), the spring water when not used for irrigation sank into a rather long shallow "lake" on the flat.

Mr. Sara held that the chubs of Fish Creek Springs are without doubt native, as indeed the name of the creek and the springs indicates. He know of no other native fish in the general vicinity, except those in springs about "Fish Lake" (obviously referring to the chubs, *Gila bicolor* subspecies, of Little Fish Lakes in a tributary valley of the Lake Railroad system, separated from Fish Creek Valley by a low divide). Presumably no waters in Fish Creek Valley other than those of Fish Creek Springs have retained native fish.

Dunes on the valley flat just off the alluvial slope a short distance to the southward, and other evidence, indicate that Fish Creek Springs arise just within a definitive level of pluvial Lake Newark, but about 45 m. below the hypothesized outlet level. Although Fish Creek Valley has discharged within historic time into Newark Valley, there is no reason to suspect that the fish-inhabited waters of Fish Creek and Newark valleys have had any postpluvial surface connection. Since the pluvial period, any surface discharge from Fish Creek Valley has presumably sunk into the central part of the old lake bed in Newark Valley, short of any connection with discharges from the fish-inhabited springs of Newark Valley. The

differentiation of *Gila bicolor newarkensis* and *G. b. euchila*, the endemic fishes of the Lake Newark system, is consistent with this view.

Springs that margin the ancient lake bed apparently provide the only habitats in Newark Valley proper that have retained native fish. These fish comprise a subspecies, *Gila bicolor newarkensis* (pp. 156–158), which we differentiate not only from *G. b. obesa* of the Lahontan system and the aberrant populations of this subspecies from two springs in the Lake Diamond drainage basin, but also from *G. b. euchila* of Fish Creek Springs. Long isolation is therefore indicated, as we have already stated.

A number of springs along both the west and east sides of the extensive alkali flat in the northern part of Newark Valley are shown on the map of White Pine County, Nevada (Ed. Millard & Son, Ely, 1930), and on the topographic maps cited above. In 1934 we examined springs that seemed likely to have maintained native fish. Those on the west side, in R. 55 E., were: near Diamond Peak (South Peak), near middle of T. 20 N. (Location G7); at Strawberry Ranch or Strawberry, in northern part of T. 21 N., 18 km. south of Simonsen (where the fish had previously died off—see below); and at Moores Ranch, about midway between Strawberry and Simonsen, as of 1938 (Location G8). On the east, two discharging springs are indicated: one, the warm spring at Billy Moore's Ranch, close to the T. 22–23 N., R. 56–57 E. corner (Location G9); the other, not examined, marked "Sulphur Spr." on the 1930 county map, southeast of the center of T. 20 N., R. 56 E. (presumably the "Barrel Spring" on the Buck Mountain Quadrangle). There are, presumably, a few mountain streamlets on the west and possibly on the east side of the valley, but the only one that seemed to be possibly propitious as a habitat for native fish is Cold Creek, which was found to be fishless (p. 157).

Characteristics of the springs retaining the native chubs in Fish Creek and Newark valleys are stated in the accounts of *Gila bicolor newarkensis* (pp. 157–158) and *G. b. euchila* (pp. 168–169). The springs at Strawberry Ranch, which had become nearly dry at the time of our visit in 1934, were reported by the rancher to have contained chubs until they had been completely killed off by freezing a few years previously.

Pluvial Lake Hubbs

Drainage basin in northwestern White Pine County, with the northwestern arm projecting into Elko County, eastern Nevada (fig. 7).

Solely on the basis of the crude maps then available and local testimony, backed by the relationships between enclosed basins and pluvial lakes in the general area, we postulated (Hubbs and Miller, 1948b, p. 59) a "lake in Long Valley," as probably small and ephemeral, and merely mapped (as no. 31) the remnant dry lake. Snyder *et al.* (1964) correctly mapped a sizable Pleistocene lake (no. 52) in the basin, naming it Lake Hubbs. Their mapping has been adopted by Feth (1961, 1964) and Morrison (1965, fig. 1).

The pointed northern tip of the Lake Hubbs drainage basin is inserted between the Lake Franklin and Lake Gale sections of the Lake Franklin watershed. The eastern edge abuts the Lake Gale basin; the southeastern margin, the Lake Jake basin; and the western side, the Lake Newark and Lake Franklin drainage systems.

The greatest length of the drainage basin is 90 km.; that of the somewhat oblong main section, roughly 58 km. The greatest width, at a bulge in the western border, near the middle of the main part, is 32 km. The sharply pointed northeastern arm, embracing Long Valley Wash, is about 40 km. long; its greatest basal width is roughly 18 km. The form of the lake closely approximated that of the drainage basin. The greatest length was 51 km.; the greatest width, both in the northern and southern sectors, was 14 km.; the least width, near middle, 12 km. The dimensions of the pointed northeastern arm of the lake were, approximately: length, 17 km.; width at mouth, 9 km.; width near middle, 3 km.

As charted by us, the area of the lake, 490 sq. km., constituted 29 percent of the area (1,677 sq. km.) of the drainage basin; roughly agreeing with the values (205 sq. mi., 32 percent of 635 sq. mi.) given by Snyder *et al.* (1964). On the basis of our altimeter estimate of 6,266 feet (1,910 m.) for the top lake level, repeatedly checked against the assigned altitude of 6,352 feet for the bench mark near the north border of T. 20 N., R. 59 E., the depth of the lake is computed to have been 206 feet (63 m.) above the present playa altitude of about 6,060 feet (1,847 m.) indicated by the Ely 1:250,000 map. This is somewhat less than the depth of 250 feet listed by Snyder *et al.*, but on a reconnaissance of the entire, well terraced eastern shore and northern end of the ancient lake, we found no trace of higher beachlines.

Such an accumulation of water is remarkable in a valley now almost completely desiccated (fig. 5). However, the basin is closely bordered by a mountain rim almost everywhere more than 300 m., and in large part more than 600 m., higher than the 1,847-m. lake bed. On the southwest side, only about 30 km. distant to the west, the Diamond Mountains rise to an altitude of 3,237 m. Furthermore, the top lake level probably was not attained in the last stages of the Wisconsin pluvial: a sample of the fluffy, pure, shell-bearing marl (discussed below) from the top terrace deposit yielded a radiocarbon measurement of more than 30,000 years B. P. (Hubbs and Bien, 1967, p. 284). Other, lower shoreline features, especially terraces and bars near the mouth of the northeastern arm of the lake, at an altitude mapped as slightly above 6,200 feet (1,890 m.), therefore at an elevation roughly 45 m. above the playa level, definitely have a very late Pleistocene appearance.

Physiographic evidence yields little or no support for an hypothesis of any underground contribution of water from surrounding basins, for the playa of Long Valley is slightly higher than the flats of lakes Newark and Franklin, respectively to the west and north, only about 30 m. lower than the playa of Lake Gale, and about 60 m. lower than the flat of Lake Jake. Furthermore, mountains intervene on all sides.

FIGURE 5. Dust rising from the playa on the bed of pluvial Lake Hubbs, in Long Valley, White Pine County, Nevada; viewed from eastern shoreline features near middle of main part of ancient lake. Photographed by senior author September 5, 1965.

The ground waters of Long Valley have been described by Eakin (1961).

SHORELINE AND DISCHARGE.

There is a strong possibility that Lake Hubbs once discharged into Lake Newark and thence through Huntington Creek and Humboldt River into Lake Lahontan. Passes to the Lake Franklin and Lake Jake watersheds are above the 6,500-foot (1,981-m.) contours, but the lowest place in the sill, Beck Pass, is shown by the Ely 1:250,000 map and the Buck Mountain 15-minute Quadrangle to be on the Hubbs-Newark divide, in Sec. 10, T. 20 N., R. 57 E., where 6,400-foot (1,951-m.) contours are separated by about 0.3 km., above the 6,360-foot (1,939-m.) contours on either side. As is indicated below, the highest beachline of Lake Hubbs that we could find was measured as about 6,266 feet (1,910 m.). However, the interdigitation of marl and gravel at the bar where this measurement was taken indicates fluctuating levels, and the marl may very well have been deposited on the exposed shore in water of considerably greater depth. That the only spill(s) may well have been prior to the last

FIGURE 6. Interbedded lacustrine marl and gravelly deltaic deposits on eastern shoreline of pluvial Lake Hubbs, in Long Valley, White Pine County, Nevada. Photographed by senior author September 5, 1965.

main pluvial period is suggested by the dating of the marl referred to above. The occurrence of freshwater mollusks (*Gyraulus* and *Pisidium*) in the marl favors a surface-water connection, but the discharge might have been through alluvium in the pass, as postulated for Lake Clover (p. 30). The lack of fish in Long Valley is not significant evidence for no discharge, because the only fish habitat that may have long persisted now periodically becomes uninhabitable (see below).

Long Valley, known to us previously only from maps and local testimony, was explored by us (the Hubbses) on September 4–5, 1965, with the great help of the Ely 1:250,000 map and a Paulin altimeter reading to 2 feet. The beach lines were examined in some detail near the middle of the east shore of Lake Hubbs, in T. 20 and 21 N., R. 59 E. The shoreline features all run roughly north–south, parallel to the lake axis and to the contours along the base of the Butte Mountains. Going north, we encountered, after seeing a slight truncation of the bajada at the valley flat, the first definite gravelly beach bars in Sec. 29, T. 20 N., R. 59 E., somewhat below the mapped 5,300-foot (1,615-m.) contour. The gravel, seemingly stratified and moderately rounded, contrasted sharply with the much sparser gravel in a road cut nearby.

About 1 km. northwest of the bench mark, with indicated altitude of 6,352 feet (1,936 m.), we found, approximately on section line 5–6, in T. 20 N., R. 59 E., a recent road-gravel pit obviously representing an ancient beach line. Again, gravel workings disclosed the level of the ancient lake. The location was estimated to be 39° 38.2′ N. lat., 115° 21.9′ W. long. Here, for the top of the bar, we obtained, by repeated checking of altimeter readings against the bench mark, an estimate of the altitude as 6,266 feet (1,910 m.), and found, close to the eastward, only a slight trace of one parallel bar, which registered the same altitude. It is convex toward the playa and appeared to be about 1 km. long. There is a weak parallel bar immediately west of the pit, and traces of other recessional levels farther toward the playa. Yellow silt deposits were exposed by a cut on the east side of the main bar.

The structure of the bar (fig. 6) had been exposed for about 6 m. vertically and 40 m. horizontally by the gravel excavation. The material was generally coarse, varying from fine deltaic gravel, in spots grading into clean sand, to coarse cobble, generally foreset but in part boldly crossbedded. In one place the gravel sharply interdigitated with, and was in part mixed with, fluffy silty lacustrine marl, which dissolved almost completely in acid. In spots the fine gravel was strongly cemented, apparently by marl rather than caliche. Fine gravel lenses occurred in the layers of marl. Some streaks rich in minute snails (*Gyraulus* sp.) and some minute clams (*Pisidium*

sp.) were found in the marl, but no trace of fish remains could be found by fracturing the marl.

Shoreline features were traced in considerable detail almost continuously from the southern to the northern border of T. 21 N., R. 59 E., over a distance of about 10 km. The highest discernible traces coincided in level with the bar just discussed, and several lower beaches were recognized. Across the valley beach features could be made out near the base of the hill in T. 20 N., R. 57 E., southeast of the low pass. A shoreline was observed near the north end of the west side of the main body of the ancient lake. Shore features were seen margining each side of the northeast arm, again somewhat below the 6,300-foot (1,920-m.) contour.

Close-set bars of relatively recent appearance extend in parallel series as gentle curves across the mouth of the northeast arm. The most southern and best defined of these, used as a road grade, carries on the Ely 1:250,000 map the elevation of 6,205 feet (1,891 m.), and the others were indicated by readings of the 2-foot altimeter to be at approximately the same elevation. These bars, of course, represent the shoreline of the lake when it surely was wholly enclosed.

The Ely and Elko 1:250,000 maps show by margined stippling a narrow sandy area 16 km. long, in the course of Long Valley Wash, that gives the false impression of a flat area. However, it is crossed by the 6,300-foot and 6,400-foot (1,920-m. and 1,951-m.) contours. The source of the sand was apparently not downwash, but deposits from dust-devils still seem to be adding to the accumulation, for many were seen rising from the old lake bed, often to be carried by southerly and westerly winds up the trough. These obviously eolian deposits apparently correspond to those at the northeastern end of the Steptoe basin (p. 56).

Remnant Waters and Lack of Fishes.

Except for flood waters, which at times shallowly cover the central playa that measures about 2×5 km. on the Ely 1:250,000 map, the only surface water on the valley floor is a spring, producing what is known as Long Valley Slough, toward the north end of the main body of the basin, near the southeast corner of T. 23 N., R. 58 E. (39° 49.6′ N. lat., 115° 23.6′ W. long.). The spring originates in a small patch of tules and other vegetation and, when examined on September 5, 1965, maintained for about 100 m. a slight flow containing much *Chara* and algae, to end in a meadow. A ranch hand at Moorman Ranch, who had trapped mustangs at the slough, informed us on June 26, 1942, that about July 1 the water "goes slick" and is then unfit to drink and needs to be cleaned out for cattle use. He had done so the previous year and was positive there were no fish in the spring. Jerome Phalan Stratton concurred, and our scrutiny revealed no fish. The extreme aridity of the valley is shown in a photograph reproduced inside the front cover of Eakin's report (1961).

There are some mountain springs in the Long Valley drainage basin, particularly near the divide between this valley and Jakes Valley, but none of them can be expected to support fish. One of these, North Spring, with a slight discharge, was examined in 1965.

Pluvial Lake Clover

Drainage basin in southeastern Elko County, Nevada (figs. 7, 11).

This well definable pluvial lake, which has been mapped since the time of Russell (1885), was named and discussed by us (Hubbs and Miller, 1948b, lake no. 26, p. 53), with a review of pertinent literature. The name Lake Clover has been accepted by Snyder *et al.* (1964) and Feth (1964).

This lake occupied an enclosed basin that is largely very flat. The basin is bounded on the north by the contiguous drainages of lakes Lahontan and Bonneville, on the east by the basin of Lake Waring, on the south by the basins of lakes Waring and Franklin, and on the west by the drainages of lakes Franklin and Lahontan.

The maximum, roughly north–south length of the western and eastern arms of the dumbbell-shaped drainage basin were approximately 59 and 79 km., respectively, and the corresponding lengths of the similarly shaped lake were about 38 and 46 km.; the east–west dimension of the joint basin was about 36 km.

At its maximum depth of about 42 m. (see below), the lake occupied 930 sq. km., or approximately 35 percent of the combined area (2,624 sq. km.) of Clover Valley to the west and Independence Valley to the east. The large extent of the lake, with the surface altitude of 740 m., is attributable to the circumstance that more than half of the periphery was closely rimmed by mountains rising to altitudes exceeding 2,000 m., with several peaks higher than 3,000 m. The East Humboldt Range, forming the western rim of the basin, is sufficiently high and far north to have been extensively glaciated in Pleistocene time (Sharp, 1938). Furthermore, Lake Clover almost certainly received considerable inflow northward from the higher Lake Franklin through the alluvium in the low pass between Valley and Spruce mountains (p. 42).

Since the alkali flat in the southern arm of Independence Valley has the assigned elevation of 5,578 feet (1,700 m.), and the top terrace was estimated at about 5,715 feet (1,742 m.), we calculate that the maximum depth of pluvial Lake Clover approximated 42 m.

SHORELINE AND DISCHARGE.

Lake Clover may have attained some subterranean discharge through alluvium in the pass at the north end of the western arm, which was only about 30 m. higher than the maximum lake level, according to altimeter readings and the contours on the Wells 1:250,000 map. There must once have been a discharge into the headwaters of the Humboldt River, however, for the valley contains differentiated minnows related to and obviously derived from cognates occurring in those headwaters, but the spill was almost surely during a pluvial period sufficiently remote to have allowed the obliteration of the high shoreline features by erosion and by deposition. The lack of any trace of an outlet channel in the gentle, mile-wide pass counters any concept of a late-pluvial surface discharge.

It is quite possible that the outlet level of Lake Clover may have approximated the level (about 5,715 feet = 1,742 m.) of the highest recognized terrace, and that the low sill between the lake bed and the watershed of the Humboldt River headwaters represents an alluvial aggradation from the mountains on either side. For this reason, we make no effort to postulate or map a discharge-level area of Lake Clover at the lowest altitude of the drainage-basin sill.

Presumably because Lake Clover did not attain and hold an outlet level in late pluvial time, the shoreline features are not very bold. Furthermore, the western shores of the west arm and of the northern part of the east arm are in the lee of very high mountains and were, therefore, little subject to wave action. In addition, the southern shore of each arm was, we assume, protected by marsh growth on the gentle slope. In some places, however, shoreline features are preserved, as along the east shore, around the tip, and along the east shore of the Spruce Mountain peninsula, and on the north side of the small island now represented as a slight hill marked on the Elko 1:250,000 map as having an altitude of 5,743 feet (1,750 m.). We encountered, in 1965, on the north slope of this knoll, a road-gravel borrow pit where a rather thick bed of fine sand and moderately rounded gravel indicated an ancient beach, as did sand dunes to the northwest and northeast at a slightly lower level. Two or three slight rises between the borrow pit and the crest of the hill (about 0.8 km. distant) seemed to represent higher lake levels, but no trace of beach features appeared on the top of the knoll, where the gravel was angular. Altimeter readings provided an estimate of 5,710–5,720 feet (about 1,742 m.) for the top beachline here. Several beach terraces around the north end of the Spruce Mountain peninsula, with the uppermost sharpest and with

no trace of any higher ones, seemed consistent in elevation. The road southward along the east side of the peninsula, mapped just below the 5,700-foot (1,737-m.) contour, closely follows sand ridges and some fine gravel ridges indicative of old beaches. The gravel pit labelled on the Wells map near the north end of Independence Valley, at the altitude of nearly 5,700 feet, is probably on a near-maximum shoreline. No indications of shores substantially higher were seen.

REMNANT WATERS AND FISH LIFE.

Except along a narrow fringe, at the foot of the surrounding slopes, the bed of pluvial Lake Clover remains as an extremely level alkaline flat. A minor part of Clover Valley (the western arm of the basin), where enclosed by the 5,600-foot (1,707-m.) contour (on the Elko map), is occupied ephemerally by Snow Water Lake, when streams flowing down the draws from the southern part of the East Humboldt Range reach the bolson. Though the major part of Independence Valley lies within the 5,600-foot contour, only "ALKALI FLAT" is mapped there, and no water was visible when we were in this valley on August 25, 1965, although exceptionally heavy rains had recently fallen in this area. The combined drainages from the many stream courses tributary in flood to Independence Valley, including the northern streams of the East Humboldt Range (see Wells and Elko 1:250,000 maps), had failed to flood the flat, though considerable water was standing in the part of the valley connecting the two arms.

There appear to be no permanent streams habitable by native fish in the drainage basin. One, in Independence Valley, as marked on the Wells 1:250,000 map, had no water where we crossed it on Highway U.S. 40, August 27, 1965. The other stream, marked as permanent, running southwestward from near the north end of the East Humboldt Range, carries no water as far as the valley. There are two large groups of springs, each known as Warm Springs, in the basin, one cluster on the west side of Clover Valley south of the middle and another group on the west side of the north arm of Independence Valley. There is another rather large spring, on the Wright Ranch (formerly the Ralph Ranch) at the southeast base of a small hill on the west slope in the far-northern part of the north arm of Clover Valley. All three of these larger springs contain relict fish, discussed below. The three habitats are described on pp. 129 and 134–135. The waters of the basin were treated, in agreement with our findings, by Eakin and Maxey (1951b).

Four glacial tarns are mapped on the Clover basin side of the divide between that basin and the Humboldt River watershed. They are no doubt too high to contain native fish, unless, as a remote possibility, trout.

In the basin we found no trace of *Relictus solitarius*, the relict endemic minnow of the Franklin-Gale and Waring-Steptoe drainage systems that adjoin the Lake Clover basin to the southwest, and southeast, respectively. This was surprising, since Lake Franklin apparently barely missed spilling into Lake Clover (p. 42). However, we found evidence that there was a subterranean discharge, through which fish could not have passed.

Instead, we took in the Clover system samples of two endemic subspecies of *Rhinichthys osculus* (*R. o. oligoporus* and *R. o. lethoporus*, pp. 129–141) and an endemic subspecies of *Gila bicolor* (*G. b. isolata*, pp. 175–180), all of which are related to forms inhabiting the extreme upper headwaters of the Humboldt River, the main affluent of Lake Lahontan. These isolated differentiates, as noted above, bespeak a discharge of Lake Clover, but at some pluvial period prior to the most recent one.

It is assumed that native fish do not occur in the Clover drainage basin at any place other than the three just mentioned. The mountain-canyon streams are assumed to be devoid of native fish, though the possibility of the retention of native trout in the streams of the East Humboldt Range has not been completely excluded. This possibility seems remote, and the explorations and inquiries

of trout-specialist Robert J. Behnke and of fishery biologists of Nevada have yielded no evidence that native trout have occurred in the Lake Clover basin. Such canyon streams often fail to reach the valley floor, and in the mountains are subject to destructively torrential precipitation.

There is also a possibility, also seemingly remote, that some cyprinids may have held out in some of the other, minor springs along the west side of Clover Valley. Mr. Vernon Westwood, who had been on Warm Springs Ranch in Clover Valley for 11 summers, testified in 1965 that the only ranches in that valley that contain native fish are the three where we found them and the "Der Weeks Ranch," which we did not examine and concerning which we obtained no information, not even its location.

The valley-bottom waters in Clover Valley are almost surely much too impermanent and alkaline for fish life. We saw none in the ample but obviously temporary waters that had resulted from unusually heavy recent rains when, in 1965, we examined the area connecting Clover and Independence valleys.

It seems certain that fish are absent thoughout the extremely arid Independence Valley, save about the cluster of Warm Springs where we took the two endemics, *Rhinichthys osculus lethoporus* and *Gila bicolor isolata*. There appear to be no permanent surface waters in the Independence Valley basin except this cluster and three very small groups of springs at the edge of the lake bed along the east side of Spruce Mountain Ridge, which separates the southern lobes of Clover and Independence valleys. On August 25, 1965, after failing to find any habitable water around the mountainous lobe separating the northern arms of the Clover–Independence graben, we became convinced that no fish exist around the southern peninsula. No springs are shown on the west shore of this Spruce Mountain lobe. The very limited discharge of Spruce Point Spring, at the tip of the lobe, was found to be fishless, as were the numerous spring sources, mostly mere seepages, of Chase Springs. Mound Spring, still farther south, was not visited, but a government trapper we encountered knew it well and assured us that it is a mere seepage, devoid of fish. He seemed to be thoroughly familiar with Independence Valley and was certain that the only minnows in the valley are those in Warm Springs (mentioned above).

PLUVIAL LAKES REGARDED AS HAVING HAD CONNECTIONS WITH BOTH LAHONTAN AND COLORADO SYSTEMS

(The Lake Railroad Complex)

One major and obviously ancient drainage basin in central Nevada, that of pluvial Lake Railroad, yields physiographic and ichthyological evidence of once having had some headwater connection with the Lahontan drainage system and as once having been a part of the Colorado River watershed. Two or more now dry and fishless adjacent basins, those of pluvial lakes Snyder (pp. 37–38) and Lunar Crater (pp. 36–37), furnish doubtful physiographic evidence of having been tributary to Lake Railroad. Little Fish Lakes (p. 36) definitely did drain into Lake Railroad, through Hot Creek Valley, which has been held, we think wrongly, to have contained a Pleistocene lake (pp. 33–34).

Pluvial Lake Railroad

Drainage basin covering several valleys over a large area in Nye County, overlapping into southwestern White Pine County and slightly into northeastern Lincoln County, in south-central Nevada (fig. 2).

This lake, which was probably the largest of those between lakes Lahontan and Bonneville and which lay in the largest of the drainage basins, was named "Quaternary Railroad Lake" by Hubbs (1941a, p. 67, fig. 6) and Railroad Lake by us (Hubbs and Miller, 1948b, pp. 90–94, 154, 164). This lake system and its fish fauna were discussed by us in some detail, with a review

of the pertinent literature. The lake has also been called "Railroad" by Snyder *et al.* (1964), Feth (1964), and others. We now prefer the form, "Lake Railroad," to conform with general usage for pluvial lakes (p. 3).

The drainage basin of pluvial Lake Railroad is bounded on the northwest and north by the basins of ancient lakes Diamond and Newark, both of which were once parts of the Lahontan system. Along most of the eastern drainage divide the tributaries of Lake Railroad abutted those of the pluvial White River, a tributary of the Colorado River; north and south of that watershed the Railroad basin is bounded on the east side respectively by the small basins of Lake Jake and Lake Coal, both seemingly dismembered from the White River system. Toward the southeast, south, and southwest, all separated by rather low divides, lie the basins of several rather ill-defined, presumably shallow, and probably more or less ephemeral pluvial lakes, in what we treated (Hubbs and Miller, 1948b, pp. 45–46, 149–150, 158–159) as the "Area of Sterile Basins," because the region seems to be devoid of native fishes and apparently was relatively arid even during the very moist period.

The Lake Railroad drainage basin measures 191 km. in length, from north-northeast to south-southwest, and 115 km. in maximum width, near the middle. The basins of two minor, probably once tributary, pluvial lakes, Snyder and Lunar Crater (pp. 36–38), form a wedge, from the north, which structurally seems to be a southern extension of the Newark graben. This wedge separates the two main affluents of Lake Railroad. The predecessors of Duckwater, Bull, and Currant creeks entered the north tip of Lake Railroad. The western affluent, which was by far the larger and longer, we named pluvial Russell River (Hubbs and Miller, 1948b, p. 92). This was obviously a very ancient stream, for its course includes two deeply entrenched antecedent water gaps. The upper section, the northwestern part of the Lake Railroad system, is becoming disjunct through the incipient graben depression that has formed Little Fish Lakes (see below), in Little Fish Lake Valley. Little Fish Lakes at high level doubtless discharged through a now usually dry structural channel that leads into Hot Creek, which follows the deep antecedent trench through the Hot Creek Range. The hot stream that arises in this trench flows at an altitude of about 6,000 feet (1,829 m.), between 7,000-foot (2,134-m.) contours separated only 1.5 km. and between 8,000-foot (2,438-m.) contours only 4.5 km. apart (interpreted from the Tonopah 1:250,000 map). The flood channel of Hot Creek then debauches onto Hot Creek Valley, where it joins a now dry channel from the north arm of that valley. After coursing through the nearly level Hot Creek Valley for 39 km., the pluvial stream entered the other water gap, notable but less spectacular, through which it passed at an altitude of about 5,100 feet (1,554 m.), between the 6,000-foot (1,829-m.) contours only 4.5 km. apart, in the mountain range designated Reveille Range to the south and Pancake Range to the north. In high flood the pluvial water course is ephemerally reconstituted.

Age-long erosion of Little Fish Lake Valley and of the gorge through the Hot Creek Range must have led to the aggradation of Hot Creek Valley, and sediment from above, supplemented by erosion in the Pancake Range, must have produced in Railroad Valley the tremendous alluvial fan that is marked on the Tonopah 1:250,000 map by 9 radiating distributaries. This fan, augmented by another large one, with multiple radial distributaries, also debauching onto Railroad Valley just to the eastward, has produced, in the narrows of that valley, the low saddle that weakly divides the basin into northern and southern playas.

These geomorphic considerations have a bearing on the interpretation of the ancient lakes and streams in the area, particularly on the existence or age of "Hot Creek Lake" and on the area covered by Lake Railroad at its highest stage.

"HOT CREEK LAKE." Snyder *et al.* (1964, lake

no. 41) and Morrison (1965, fig. 1), mapped a Pleistocene lake in Hot Creek Valley and named it "Hot Creek Lake." They indicated that it covered 88 sq. mi., in a 1,437-sq. mi. basin and that it spilled into Lake Railroad. Indeed, the area still does so discharge in great floods, but by direct surface drainage with no extensive ponding. The Tonopah 1:250,000 map shows the 5,100-foot (1,554-m.) contour penetrating through most of the gap, whereas the 5,300-foot (1,615-m.) contour coincides with the lake margin as mapped (except, of course, near the outlet). It seems to us that it is unreasonable to conclude that any lake, least of all a late Pleistocene one, existed here. We saw no trace of lake terraces in Hot Creek Valley, nor would we expect any there. We interpret the silt deposits in the valley as of flood-water, not lacustrine, origin. A very early pluvial lake might have existed here, but, if so, we saw no sign of it, and it would seemingly not have existed, unless possibly in some much earlier hydrographic era.

Concerning this supposed lake Rush and Everett (1966, p. 10) have stated, in apparent confirmation of our view:

> Snyder and others (1964) show an 88 square-mile Pleistocene lake near Twin Springs Ranch in Hot Creek Valley that spilled to Railroad Valley. The surface materials of this area are silt and clay, similar to those deposited in lakes, but no shore or beach features were recognized by the writers; therefore the lake is not shown on Plate 1. The log of well 4/51-13d1 (table 13) indicates the presence of only thin beds of lake-deposit type material rather than the thick beds usually found where a large and persistent lake occupied an area.

We add that we have often seen silt and clay deposits, in places thick, on flat desert areas that surely never held a lake.

LAKE RAILROAD, ONE OR TWO? Observations of shorelines along the alluvial slopes well above the now dry lake bed of Railroad Valley, near the center of T. 8 N., R. 55 E., just northwest of Locke Ranch, and on the east side of the valley from near Currant to south of Nyala Ranch, when reviewed with the Lund 1:250,000 map, lead us to place the highest lake shore not far below the 5,000-foot (1,524-m.) contour. A huge longshore, coarse-gravel bar (shown in our 1948b report, fig. 12), which is just east of the road, 12 km. south of Currant, seems to be, at the top, close to the 4,900-foot (1,493-m.) contour. Since according to observation and local testimony the saddle between the two dry lakes of Railroad Valley is very gentle, and the 5,000-foot contours remain well separated here, we think it probable that the lake passed through the narrows. If it did not, at the late high stage, the block probably was caused by the conjoining aggradation of the two alluvial cones mentioned above. We therefore map Lake Railroad as one, with an area greater than previously estimated, rather than as two, as shown by us in 1948 and by Snyder *et al.* in 1964 and by Morrison (1965, fig. 1). During late recession stages, at least, the lake must, however, have become separated into the two basins. Although the more southern of the two was in Railroad rather than Reveille Valley, the residual dry lake is labelled Reveille Lake on some maps, and Snyder *et al.* applied the name Reveille to the lake as a Pleistocene entity. If and when separated, the name Lake Reveille may be applied to the southern lake. For present purposes, however, we treat it as essentially an integral part of pluvial Lake Railroad.

On the basis just indicated, we estimate the length of the lake (north-northeast to south-southwest), at the highest stage, as 102 km.; the greatest width 24 km. in the main area, 10 km. in the southern expansion. The width in the narrows was probably only 2 to 5 km.

The depth of the lake above the altitude indicated as 4,635 feet (1,413 m.) for the present playa would have been 340 feet (104 m.) if the highest surface altitude was 4,975 feet (1,516 m.). We regard this as a good approximation. Snyder *et al.* (1964) listed the depth of Lake Railroad as 315 feet (96 m.), but gave no value for Lake Reveille.

The area of the lake, as we now chart it, was 1,394 sq. km., or 13 percent of the 10,874 sq. km. of the drainage basin, or 11 percent of the basin (12,343 sq. km.) if the drainage areas of lakes Snyder and Lunar Crater be included.

In view of the height of the mountains that largely border the drainage basin, and slice into it in places, this vast accumulation of water is plausible, even though the area is transitional between the belts of great and only moderate pluvial accumulation of surface water. The ridges generally rise above the altitude of 2,500 m. and in several places exceed 3,000 m.

The hydrography of most of the basin has been outlined by Maxey and Eakin (1951) and of the western part by Rush and Everett (1966).

Remnant Waters and Fish Life in the Lake Railroad System, and Probable Past Drainage Connections.

Our summary (Hubbs and Miller, 1948b, pp. 90–94) presented in moderate detail an account of the dribbling remnant of surface waters in the Lake Railroad system, and made it clear that the basin is inhabited by only two species of native fish, namely a cyprinodontid, *Crenichthys nevadae* Hubbs (1932), which is closely related only to *Crenichthys baileyi* (Gilbert) of the remnant waters of the pluvial White River division of the Colorado River system, and a cyprinid (now called *Gila bicolor*), which is a representative of the Lahontan fauna. We further pointed out that in only one other pluvial drainage complex, that of the Death Valley system in eastern California and southwestern Nevada, have the Lake Lahontan and Colorado River fish faunas become intermingled through vagaries of past hydrographic connections (Miller, 1946, 1948; Hubbs and Miller, 1948b, pp. 77–88, 152–153, 162–163, figs. 20–22). We also indicated that present topographic relations seem to negate the idea that such connections existed during late Pleistocene time. The superior topographic information now available can be brought to bear on the problem of the past hydrographic and fish-faunal connections between the Lake Railroad system and other drainage basins.

One possible route that might have been followed in the dispersal of the chub species *Gila bicolor* from its central distributional location in the Lahontan system into the Lake Railroad system now becomes evident. The small basin of pluvial Lake Snyder (pp. 37–38) straddles a low divide between the basins of Lake Newark, a former tributary of the Humboldt River still retaining forms of *G. bicolor*, and the Lake Lunar Crater basin, which presumably once, perhaps in pre-Sangamon time, led into Railroad Valley (pp. 36–37). Very possibly the Lake Snyder basin first discharged into Newark Valley and then was captured by a former tributary of Railroad Valley through accelerated erosion in that direction, that resulted from the circumstance that the bed of Lake Railroad is more than 400 m. lower than that of Lake Newark. As we have previously surmised (Hubbs and Miller, 1948b, p. 91), this possible dispersal channel may have been less remote geologically than the connection suggested by the northward-downsloping canyons observed in the southern drainage on the Duckwater-Newark divide.

We pointed out in 1948 that a past connection between Railroad Valley and the Colorado River was suggested by the intervening chain of desert valleys separated by low divides. The topographic information now presented on the Goldfield and Caliente 1:250,000 maps and the U.S.G.S. 1:500,000 topographic map of Nevada (1965) essentially confirms the postulated route, but supports the idea that the connections existed prior to the present state of development of the Basin and Range geomorphology, for the valleys seem separated by divides presumably too high for surface-water crossing. The lowest divides out of the Railroad Valley depression, lying between the 5,600-foot and 5,800-foot (1,707-m. and 1,768-m.) contours, are southward into the cul-de-sac basin of pluvial Lake Kawich and into the basin of Lake Penoyer, farther east. From Penoyer (Sand Spring) Valley the low passes,

between 5,400 and 5,600 feet (1,646 and 1,707 m.) lead into Tickaboo (Desert) Valley either directly, or indirectly through the basin of Lake Groom in Emigrant Valley. Tickaboo (Desert) Valley, with a dry-lake bed altitude of less than 1,070 m., leads *via* a low-level pass into Pahranagat Valley, in the course of pluvial White River (see the 1:500,000 map of Nevada). The known occurrence of the genus *Crenichthys* Hubbs (1932) only in the Lake Railroad and pluvial White River systems, and the full specific differentiation of the species in the respective basins, fits nicely into the hydrographic evidence, as we have already pointed out (Hubbs, 1941a, pp. 66–68, fig. 5; Hubbs and Miller, 1941, p. 2; 1948b, pp. 90–93, fig. 24).

We have already indicated (Hubbs and Miller, 1948b, pp. 90–92) that the fish fauna of the Lake Railroad system consists of a series of local differentiates of the cyprinid now called *Gila bicolor* (pp. 72, 142) and the entire population of the cyprinodont *Crenichthys nevadae* (pp. 227–229). The distribution of the various spring populations was briefly outlined. More detailed treatment is reserved for a future publication.

Pluvial Little Fish Lakes

Snyder *et al.* (1964), followed by Morrison (1965, fig. 1) and by Rush and Everett (1966, p. 10), showed two small Pleistocene lakes in Little Fish Lake Valley, the westernmost arm of the Lake Railroad system (fig. 2). Snyder *et al.* listed the lakes as no. 51, without assigning a name, and estimated their area as 4 sq. mi. (10.4 sq. km.) in a drainage basin of 467 sq. mi. (1,210 sq. km.). Our measurements are 11 sq. km. for lake area, constituting 1 percent of the area (1,131 sq. km.) of the drainage basin, which measures 25 × 60 km. Snyder *et al.* correctly indicated that these lakes spilled into Hot Creek Valley, but only at the maximum stage. The Tonopah map shows Fish Lake as permanent but little more than 1 km. long, and above and below it, ephemeral lakes, respectively 2.5 and 1 km. long. On September 7 of 1934, a year of intense drought, Fish Lake was an almost completely dry alkali flat, but showed signs of having overflowed. The two supposed ephemeral lakes were seen to be merely meadow areas. The southern and the middle lakes apparently together represent the larger of the two minute pluvial lakes portrayed by Snyder *et al.* and now by us. The past and present hydrography of the basin has been treated by Rush and Everett (1966).

Remnant Waters and Fish Life.

The hydrographic and ichthyological evidence for this area was briefly treated by us (Hubbs and Miller, 1948b, pp. 91–92). A subspecies of *Gila bicolor* that occurs in springs about the least desiccated of the remnants of the Little Fish Lakes seems to be closely related if not referable to the subspecies occupying Twin Springs in Hot Creek Valley and a population in Duckwater Creek (the only place where *Gila bicolor* and *Crenichthys nevadae* seem to have occurred together). The same type has appeared in the outflow of Artesian Well 7 on the playa of Lake Railroad, presumably by flood connections from either Twin Springs or Duckwater Creek, although local testimony, following common precedent, ascribed the origin of the population to artesian outflow.

Pluvial Lake Lunar Crater

Drainage basin in Sand Spring Valley of Nye County, west of Railroad Valley (not to be confused with Sand Spring or Penoyer Valley in Lincoln County); in south-central Nevada (fig. 1).

The very small pluvial lake that was placed in an area carrying question marks on our 1948 map (because the mapping was inadequate), was shown, without being named, as a Pleistocene lake on the map by Snyder *et al.* (1964), which has been repeated by others, also without assigning a name. It was mentioned, but shown only as a playa border, by Rush and Everett (1966, p. 10, pl. 1). We propose that it be called Lake Lunar Crater, from

the name of the most prominent of the several conspicuous craters in the area.

The drainage relations are far from certain. At times, the drainage basin may have received a discharge from pluvial Lake Snyder (see below), and Lake Lunar Crater itself may have discharged into Lake Railroad. But, on the assumption that the drainage was endorheic, as it almost surely was at less than maximum lake level, the basin was bounded on the east and south by the Lake Railroad watershed and on the west, successively from south to north, by the drainage basins of lakes Railroad, Snyder (perhaps tributary), and Newark; and the pointed north end splits the Newark and Railroad tributaries.

The elongate drainage basin measures 82 km. from north to south and, north of middle, 25 km. in maximum width (or 29 km. if the basin of Lake Snyder be included). As mapped, very possibly considerably too small, just beyond the margins of the contained lake, the lake measured only 2.5 × 5.5 km., and covered an area of only 11 sq. km., less than 1 percent of the area of its drainage basin (1,321 sq. km. without, or 1,469 including, the drainage basin of Lake Snyder).

Even though the area is now extremely arid, and even in pluvial time was presumably relatively dry, this ratio of lake-to-basin area seems incongruously low, especially when we note that some high mountains margined the valley. It seems plausible to assume that the lake was either considerably larger than indicated, or that it discharged, either on the surface or through alluvium or lava, into a tributary to Lake Railroad. The discharge may have been temporary or intermittent, or may have occurred prior to the last pluvial. We note on the Tonopah and Lund 1:250,000 maps that the lake basin is separated from the Railroad watershed to the south by a low and rather broad, flat area in the Pancake Range. This flat area is crossed by the 5,800-foot (1,768-m.) contour, which just margins the playa that is taken to represent the ancient lake. That contour is mapped as not passing through the low, narrow hill ridge (of lava?) to the east, that separates the Lunar Crater basin from the Railroad Valley playa, 1,165 feet (355 m.) lower. Local testimony in 1938 confirmed the indication that the basin of the playa that we now treat as the remnant of Lake Lunar Crater leads southward across a very low divide into "Mosquito Flat" (formerly "Little Round Valley"), which in flood drains into Railroad Valley. Whether the ancient lake discharged is highly uncertain.

The hypothesis that a pluvial lake did accumulate in Sand Spring Valley is supported by the great extent of the drainage basin, by the definitively indicated playa, and by the height of the surrounding mountain rim, which includes, near the north end, Moody Peak. That peak is assigned the altitude of 8,888 feet (2,709 m.) on the United States Geological Survey map of the State of Nevada 1:500,000 (1965) and the height of 8,935 feet (2,723 m.) on the Ely 1:250,000 map. The suggestion on the Tonopah map of a cross bar, immediately southwest of the playa edge, seems confirmatory.

Observation of the area by binoculars from near the highway (U.S. 6) that crosses the basin a few kilometers north of the lake bed (and north of Lunar Crater) gave no suggestion that any permanent waters capable of having maintained native fish exist in this basin.

Pluvial Lake Snyder

Drainage basin in Nye County, Nevada, northwest of Railroad Valley (fig. 2).

This small pluvial lake was not treated in our 1948 report, because we had not visited the area, and no topographic map was available. The basin was shown, with a contained Pleistocene lake, by Snyder *et al.* (1964) and by Morrison (1965, fig. 1), and Rush and Everett (1966, p. 10), but no one has named the lake. We propose that it be termed Lake Snyder, as a token recognition of the notable contributions that Charles T. Snyder of the United States Geological Survey has made to the paleohydrography of the Great Basin.

The drainage basin is bounded on the northwest and north by the watershed of Lake Newark; on the east and southeast, by that of Lake Lunar Crater (just treated); and on the west by the Hot Creek Valley division of the Lake Railroad drainage basin.

The basin is irregular in outline and greater in north-to-south than in east-to-west dimension, as was the lake. The basin is 20 km. long and 13 km. in greatest width; the lake, as mapped, was 11 km. long and 5 km. wide.

In the tabulation accompanying their map, Synder *et al.* (1964) listed the area of the lake as 10 sq. mi.; that of the basin, as 69 sq. mi.; and the depth as "shallow." On the basis of plotting the lake boundary along the 6,500-foot (1,981-m.) contour on the Tonopah 1:250,000 map, as Snyder *et al.* apparently did, and as seems reasonable since this contour is shown margining what was almost certainly a major longshore bar, we estimate the area of the lake, in essential agreement, as 24 sq. km., but we estimate the area of the drainage basin, by use of said map, as somewhat smaller (148 sq. km.). On this basis, we compute the area of the lake as 16 rather than 14 percent of the area of the drainage basin.

The circumstance that the tributaries came from outlying ridges of the high Hot Creek Mountains to the west renders plausible the existence of a pluvial lake in the basin. More compelling is the indication, mentioned above, of a gently curving bar extending from the east across most of the northern part of the valley flat.

There is no indication that any other basin discharged into Lake Snyder, but we note that a branch of the main former tributary of Lake Lunar Crater is shown on the Tonopah and Lund 1:250,000 maps as passing within about 1 km. of the southern border of the lake. However, we may well have mapped the border too low, for the contour line (6,500-foot) used for the lake shore is shown on the probable bar, which presumably formed under water. It is our provisional and questionable hypothesis that the lake at its highest level did discharge into Lake Lunar Crater, and from there very possibly into Lake Railroad (see above).

The possibility that Lake Snyder may have discharged northward into the Little Smoky Valley arm of the Lake Newark drainage basin, rather than into Railroad Valley, is not excluded by the contours on the Tonopah map, because the 6,500-foot (1,981-m.) contour used to define Lake Snyder is not separated by any other contour from the next 6,500-foot contour to the north (the one mislabelled "6,700" on the map). In fact, the Lake Snyder basin conjoins the main part of Little Smoky Valley and Sand Spring Valley of Nye County, within a single sublinear depression. In at least some local usage, learned in 1938, the Lake Snyder basin is regarded as part of Sand Spring Valley.

Another rather fascinating possibility, suggested above (p. 35), as an explanation of the establishment of the Lahontan species *Gila bicolor* in Railroad Valley, is that the waters in the Lake Snyder basin first drained northward into Humboldt River *via* the Newark basin, and later were captured by the waters flowing southward, probably at some early pluvial period, into the much lower basin of Lake Railroad.

Knowing how arid the general region is at present, we think it almost certain that the basin of Lake Snyder lacks permanent water capable of supporting native fish life, and no hint to the contrary was given by our local informers.

PLUVIAL LAKES CONTAINING THE RELICT DACE (BETWEEN LAHONTAN AND BONNEVILLE SYSTEMS)

Two enclosed drainage systems, each occupied by two pluvial lakes that were connected by stream flow, are of central interest in the present study. These are the Lake Franklin system, containing lakes Franklin and Gale, and the Lake Waring system, containing lakes Waring and Steptoe. The very minor pluvial Upper Lake Steptoe is interpolated along the course of Steptoe River, the main feeder of Lake Steptoe. Lake Antelope, of

moderate size, occupied a basin that was presumably dismembered from the Lake Waring basin.

The Lake Franklin and Lake Waring systems, which must have had either some distributary connection over the intervening divide, or, less plausibly, an extremely remote direct connection, comprise the entire present native range of the relict dace, *Relictus solitarius* (pp. 196–207).

Pluvial Lake Franklin

Drainage basin in southern Elko County and (slightly) in northern White Pine County, Nevada (figs. 7, 11).

Pluvial Lake Franklin, one of prime interest, both geomorphologically and faunistically, was named by Sharp (1938), and was discussed by us (Hubbs and Miller, 1948b, pp. 52–53) with a brief review of the pertinent literature.

This lake occupied a largely very flat basin that, so far as is apparent (see below), did not quite attain a surface discharge, at least in late pluvial time. The northeastern rim of the basin adjoins that of pluvial Lake Clover (pp. 29–31). The middle of the eastern border adjoins the basin of Lake Waring (p. 46). The remainder of the rim, on the southeast side, is coterminous with the north end of the tributary graben of pluvial Lake Gale (p. 45) and with the northeastern arm of the enclosed basin of Lake Hubbs (p. 26). On the west, the basin is bounded by the great fault-block escarpment of the lofty Ruby Mountains, the less abrupt western slope of which is drained by headwaters of the Humboldt River, the chief feeder of Lake Lahontan. Lake Clover was once also tributary to the Humboldt, and Lake Hubbs may have been, by way of the Lake Newark basin. Far to the south the drainage basin of the tributary Lake Gale contacts pluvial tributaries to, or basins disjunct from, the watershed of the Colorado River.

The Lake Franklin drainage basin is weakly curved along the western escarpment, is roughly pointed at each end, and has a maximum straight-line length of 112 km. The longer, western part of the basin (Ruby Valley) is linear, but medially the basin is extended eastward, in squarish form, to embrace the lower, northern end of Butte Valley, which in pluvial time received the discharge of Lake Gale, through a short stream that we now name pluvial Butte River. The width of the central part of the basin is 43 to 57 km.

The lake itself roughly followed the form of the basin. The main, western part, 84 km. long, comprised a south-end expansion about 11 km. wide and 15 km. long, a connecting strait 5 to 7 km. wide and 11 km. long, and the major body of water, which was expanded in roughly triangular form eastward. Beyond a constriction only 5 km. wide, between projecting points, the lake moderately expanded into the eastern arm, in Butte Valley. Here the impoundment was once thought to have been a separate lake, but it was called pluvial Butte Bay by us (Hubbs and Miller, 1948b, pp. 52–53). This bay, which was hooked southward, was 29 km. long, and at its southern tip received pluvial Butte River. The greatest width of the whole lake was 38 km.

At its maximum depth of 53 m., Lake Franklin occupied about 1,314 sq. km., 25 percent of the entire drainage basin area (about 5,271 sq. km.), including the hydrographic area of the tributary Lake Gale basin (next section), and 39 percent of the drainage area (3,338 sq. km.) excluding that subbasin. The depth (above present playa surface) was estimated by Snyder *et al.* (1964) as 210 feet (64 m.), which approximately agrees with our interpretation, for the lowest playa elevation given on the Elko and Winnemucca 1: 250,000 maps is 5,939 feet (1,810 m.) and we found the highest beach line (see below) to be somewhat above the mapped 6,100-foot (1,859-m.) contour. C. T. Snyder (personal communication), by field work in 1969, has placed the level as 6,113 feet (1,863 m.), yielding a water-depth estimate of 53 m.

This tremendous water storage during the pluvial periods is attributable to the northern location and to the great height of the surrounding

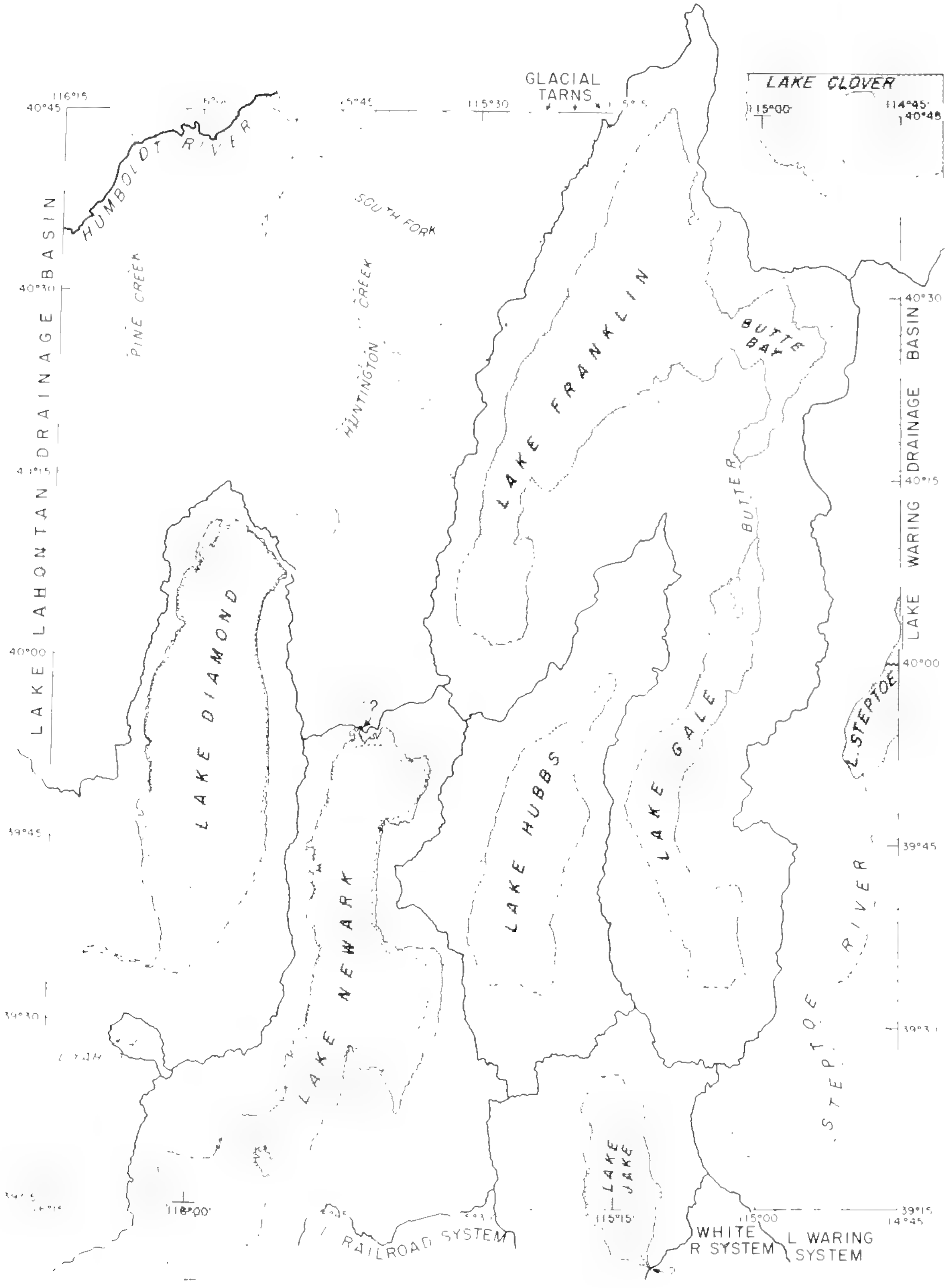


FIGURE 7. Detail of pluvial hydrography of central part of study area ('C' on fig. 1).

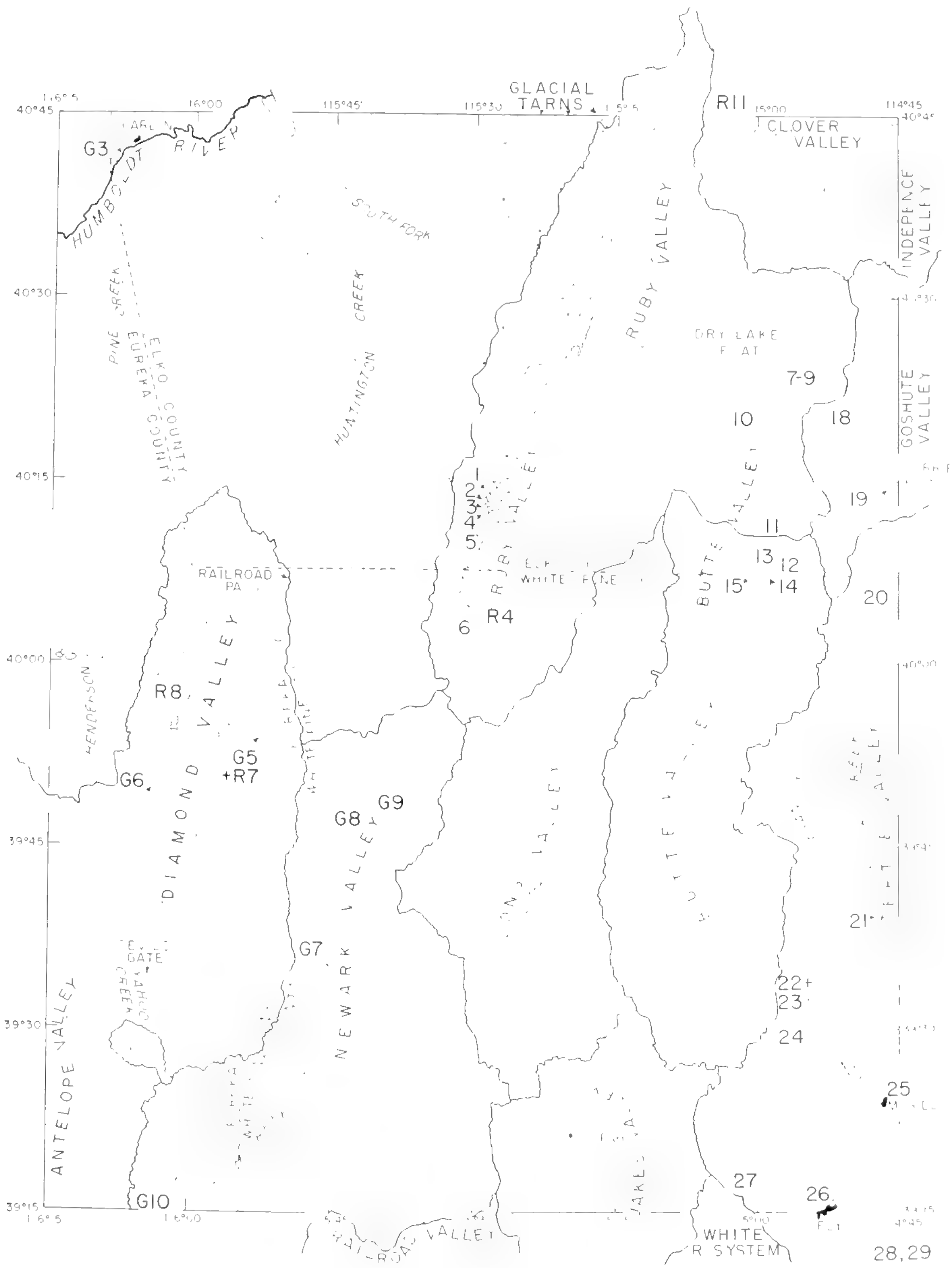


FIGURE 8. Detail of modern hydrography of central part of study area ('C' on fig. 1): showing also key geographic features, Locations for *Gila* (G–) and *Rhinichthys* (R–), and Collections for *Relictus* (–).

mountains. Except in a few narrow passes, the entire abrupt west rim of the depression lies above the 7,000-foot (2,134-m.) contour, and several peaks reach an altitude of 3,000 to 3,378 m. This range (Ruby Mountains), along with the contiguous East Humboldt Range (which contributed to the Lake Franklin watershed at the extreme north end), comprised the most extensively glaciated area within the Great Basin (Sharp, 1938), between the Sierra Nevada and the Wasatch Range. Five more or less separated lesser ranges, each rising to altitudes above 2,400 m., and several other small and less elevated mountains, supplied direct inflow from the east, and the tributary Lake Gale was almost completely flanked by high mountains.

As is indicated below, Lake Franklin did not rise high enough to attain a surface discharge through any of the four passes. The divides southward toward Lake Hubbs, northward then westward into the Lake Lahontan drainage, and eastward toward Lake Waring, were all definitely too high to have effected an outflow. The pass between pluvial Butte Bay and Lake Clover, however, was so low that a spillage in that direction has been suspected, but apparently was not quite attained. In our previous report (Hubbs & Miller, 1948b, p. 52), referring to this pass, we stated that our "altimeter readings indicate that at its maximum height Lake Franklin here rose to within 20 feet of the lowest summit, in Wells Fargo Canyon" (the name given on old maps to the pass between Valley Mountain and Spruce Mountain). The initial reconnaissance, of June 27, 1942, which led to this conclusion, was repeated by us in more detail on August 26, 1965. After just passing over the very gentle saddle southward we were fortunate enough to encounter extensive road-gravel works (at the northern tip of Butte Bay as charted on fig. 11—a point located by compass triangulation). Gravel had obviously been excavated here for fills on U. S. Highway 93. Here, well removed from any ancient stream flow, running crosswise of the pass, well rounded gravel, rather uniform in size, formed a deposit about 5 m. thick. All indications are that this beachline represents a long stillstand of pluvial Lake Franklin. The level seemed to correspond with the highest of the beachlines that are visible around the entire periphery of ancient Butte Bay, including the areas just southward and just southwestward. A line of test pits extending northward across the summit of the gentle saddle (about a mile distant) apparently failed to locate a supply of gravel, for none appeared in the excavated material, except for fine gravel on a low mound about 1 m. high and 10 m. in diameter within 100 m. of the divide. This engendered a second thought until the same type of gravel was found at the surface at higher elevations extending up into a draw in Valley Mountain. This gravel, which markedly increased in thickness westward, obviously had been formed by stream action on the mountain slope and had been deposited largely in an alluvial fan atop the divide, with surface sloping downward toward the east. Furthermore, the mixture of some coarse rounded gravel with much finer gravel and a large component of silt did not have the constitution of a beach deposit. The mound mentioned above and other patches on the flat pass were obviously remnants of superficial deposits that had elsewhere been eroded away. Many little gullies, running in both directions from the divide, following the recent unusually heavy rains, showed that during postpluvial time the pass must have been subjected to much erosion and presumably to considerable lowering in elevation. Therefore, the elevation of the pass above the highest Franklin beachline was probably somewhat greater than present topography would indicate.

Closely spaced readings with a Paulin altimeter marked in 2-foot intervals indicated that the divide was 44 feet (13.4 m.) higher than the top of the gravelly beach deposit (rather than 20 feet as previously estimated). Furthermore, the total lack of any outlet channel across the gentle divide (the lowest in the margin of the Lake Franklin basin) confirms the assumption that there was no pluvial surface spill. We strongly suspect that there was a subsurface discharge into the lower Lake Clover. Along the canyon leading down to

the bed of that lake there are numerous indications of higher land levels, suggesting extensive stream-channel erosion. Prior speculations regarding the drainage of Lake Franklin, dating from before adequate topographic surveys, were mentioned by us (Hubbs and Miller, 1948b, pp. 52–53). Snyder *et al.* (1964) questionably indicated a discharge at maximum lake level only. The outlet is indicated on Morrison's (1965, fig. 1) map.

The failure of Lake Franklin to overflow is also strongly indicated by the lack in the Lake Clover basin of *Relictus solitarius*, the single native fish of the Franklin basin, and the lack in the Franklin basin of the Lahontan derivatives comprising the fish fauna of the Clover basin, and of other basins now disjunct from the Lahontan system.

C. T. Snyder's estimate of 6,113 feet (1,863 m.) for the highest level of Lake Franklin (see above) is consistent with the height of the top terrace all around pluvial Butte Bay and on the east side of the southern arm of the main body of the lake, particularly on the northwest side of Station Butte, where a beachline seemed to be visible above the marsh level. Elsewhere along the west shore of the ancient lake the pluvial beachlines are very poorly developed, presumably because this shore lay in the lee of the towering Ruby Range. Near the north end of the old lake bed, we detected in 1942, from the main road crossing to the mouth of Pole Creek (the northern head of Franklin River), seven bars, some well defined, on the eastern side. These bars lie at altitudes between the 6,000-foot and 6,100-foot (1,829-m. and 1,859-m.) contours on the Elko map (our altimeter readings were consistent with these indications).

Possible Stream Connection Between Basins of Lakes Franklin and Waring.

Although the basins of pluvial lakes Franklin and Waring are separated by a definite saddle entirely across Goshute Pass, some means of fish transfer across this divide seems to be called for, in view of the native occurrence of the distinctive endemic minnow, *Relictus solitarius*, solely, and with no marked differentiation, in the Franklin-Gale and Waring-Steptoe drainage basins. In our 1948 monograph (p. 55) we noted that:

> slight drainage channels from the mountain to the southwest flow over the nearly flat alluvial slope perpendicularly to a definite, though small and shallow valley, which, oddly, crosses over the nearly flat divide between the two basins. Pluvial streams, possibly large and permanent enough to have harbored dace, would presumably have wandered back and forth across the fan, swinging the drainage now toward Butte Valley, now toward Steptoe. The little valley crossing the divide looks like a stream channel, but if so, it can hardly represent a pluvial channel since the divide lies far above the highest pluvial lake terraces on either side. The trough may have been formed by faulting.

These observations were made near the north end of a hill perched on the divide. Another place where, much more plausibly, the relict dace may have been transferred across the Franklin–Waring divide, in either direction, was observed by us on August 26, 1965, about 5 km. to the northward, where intermittent streams slightly entrench the bajada around the south end of Spruce Mountain. One channel now leads southward, then eastward (leftward) toward Nelson Creek, which was flooded by Lake Waring, but the lay of the alluvial fan here made it seem almost certain that the channel had flowed at times to the right, into Butte Bay of Lake Franklin (see Elko map). We strongly suspect that the transfer of fish did take place here, but we find no basis for favoring a transfer from west (Lake Franklin basin) to east (Lake Waring basin), or a movement in the opposite direction. *Relictus* now occurs in spring streamlets about 12 km. distant on either side of the divide.

The occurrence of the highly distinctive relict dace in the Franklin and Waring drainage systems, and nowhere else, might be cited as evidence that these basin complexes were parts of an integrated river system prior to their separation by the

processes that have produced the Basin and Range physiography. However, since such physiographic reorganization, if it occurred, would have been in geologically remote time, it would strain plausibility to assume that the populations in the respective basins would have remained so long without any notable differentiation.

Remnant Waters.

The ground and surface waters of Ruby Valley were treated by Eakin and Maxey (1951a).

Consistent with its location at the foot of high mountains, especially the formerly well glaciated Ruby Mountains to the west, this basin is, in parts, one of the least arid in the Great Basin. In the southern third of the main western part of the valley floor there are many ponds and marshes, which presently are largely included in the Ruby Lake National Wildlife Refuge, wherein hordes of waterfowl find protection. These waters, representing the ground-water level, very largely cover the southern strait mentioned above and the western half of the southern bulge of the bed of Ruby Lake proper. The lake appears from maps to have become disrupted in dry periods, until through recent diking and other management practices the level on the Wildlife Refuge has been more or less maintained. The lake is fed by large numbers of small to large springs of clear water that issue in file along the obvious fault line near the western edge of the valley floor, over a distance of about 13 km. Cave Creek, seemingly the only permanent stream reaching the old lake bed in the southern third of the basin, emerges, almost ice-cold, from a large limestone cavern on the west side. More or less ephemeral playa ponds, shown on some maps as "Ruby Lake," occur near the north end of the ponds and marshes, where the old lake bed opens into a wider area. The ephemeral, elongate present Franklin Lake in the western part of the valley, at about mid-length, is mapped as 13 km. long. Occasionally, the bed of this lake is shallowly refilled by the flood-water discharge of several short mountain streams from the west and by several even smaller and mostly intermittent streams from the Ruby Mountains and the East Humboldt Range around the north end of the basin. On June 28, 1942, Franklin River and Pole Creek had an ample flow of clear water well out onto the old lake bed, but both tend to dry up there.

A number of valley springs (fig. 49) with considerable discharge tend to maintain Butte Creek, on the Lake Franklin (lower, northward-draining) section of Butte Valley (along the course of pluvial Butte River), but this streamlet now ordinarily disappears before it reaches the extensive Dry Lake Flat, the floor of ancient Butte Bay. The other stream channels debauching onto this lake flat are intermittent. The hydrography of this entire area has been extensively described and mapped in the report by Glancy (1968). The general aridity of the sagebrush-covered northern Butte Valley, broken by scattered marshy oases, is well shown on the cover illustration on the same report. Such conditions are rather typical of much of the area covered in the present study.

The various fish habitats in the Lake Franklin drainage are dealt with in greater detail in the section on Material Examined and Population Status, in the account of *Relictus solitarius* (pp. 196–207).

Of the series of glacial tarns near the Franklin-Humboldt divide (shown as dots on figs. 7 and 8), only one, Robinson Lake, the spring-fed source of Robinson Creek (in Sec. 23, T. 33 N., R. 59 E.), is on the Franklin side of the divide. It presumably is too high for native fish. It should be checked, however, for native trout, although state fishery employees (and we) doubt their occurrence.

Fish Life.

The only native fish of the Lake Franklin basin is the relict dace, *Relictus solitarius* (pp. 196–226). That this species is native in the Lake Franklin basin is indicated by the following statement by King (1878, p. 504): ". . . . Ruby Lake . . . . is predominantly a carbonate one, but it is of such a weak solution that fish are able to live there."

The possibility, we think remote, that a second species of minnow occurred in Ruby Lake was suggested by local testimony (p. 209). *Relictus solitarius* very probably occurred, originally, throughout the springs and marshes of and immediately feeding into Ruby Lake, and in the springs and their outlets in the northward-draining (and also southward-draining) waters of Butte Valley (fig. 49). No fish were found in Cave Creek in 1934, either within or without the deep cave, nor in Franklin River or Pole Creek, when they were flowing strongly on June 28, 1942. Trout, apparently all introduced, now occur in the short streams draining from Ruby Mountains toward the old lake bed, and bass and other warm-water fishes have been stocked in Ruby Lake, where they have very greatly depleted, though they apparently have not yet completely eliminated, the relict dace. We found no indication that exotic fish had been stocked in the springs in the northward-draining part of Butte Valley. Details regarding the distribution and habitat of *Relictus solitarius* are given in the account of that species (pp. 196–208).

Pluvial Lake Gale

Drainage basin in north-central White Pine County and extreme southern Elko County, occupying the major southern part of Butte Valley, eastern Nevada (figs. 7, 11, 13).

This lake, not to be confused with "Butte Lake," which turned out to represent a bay of Lake Franklin, was discovered and named by us (Hubbs and Miller, 1948b, p. 53, lake no. 25). The name Lake Gale has been accepted by Snyder *et al.* (1964, lake no. 10) and by Feth (1964). When the lake was discovered, only the northern end was seen, and from the distance its bed was erroneously thought to be closed in only about 30 km. from its north end. Snyder *et al.* have shown the lake to have been about thrice as long; its broadest and deepest section, now represented by an extensive playa, is toward the south end.

The drainage basin of Lake Gale is bounded by the watersheds of other pluvial lakes as follows: on the north, by Lake Franklin only; on the east, very shortly by the Lake Waring division and elsewhere by the Lake Steptoe division of the Lake Waring watershed; on the south and southwest, by tributaries to Lake Jake; and on the west, by the drainage basin of Lake Hubbs.

Both the drainage basin and lake, as is usual for minor divisions of the Great Basin, are elongated north–south, but both are distinctively arched toward the west. The greatest straight-line length of the basin is 80 km.; the maximum width is 25 km. in the northern part, 29 km. in the southern; the minimum width near the middle is 19 km. Corresponding measurements for the lake are 67 km. in length; 8 and 12 km. in greatest width, in north and south respectively; 4.5 km. in least width, north of the middle.

At the maximum outlet level, the lake is estimated to have had an area of 474 sq. km., or 25 percent of its drainage basin (1,933 sq. km.). The greatest depth that the lake attained above the present level of the playa in the southern expansion of the lake bed, where the Ely 1:250,000 map shows an altitude of 6,161 feet (1,878 m.), must have been about 35 m., for the outlet level was only slightly below the 6,300-foot (1,920-m.) contour. The estimate of 80 feet (24 m.) by Snyder *et al.* (1964) seems too low.

So great an accumulation of water is attributable to the height of the closely margining mountain ranges, which, except in narrow passes and in the narrow northward continuation of Butte Valley, consistently rise far above the 7,000-foot (2,134-m.) contour, with peaks shown as high as 9,032 feet (2,753 m.) to the west and 10,542 feet (3,213 m.) to the east.

No inflow from any surrounding basin is suggested, for the drainage divides are definite and Lake Gale was higher than any of the surrounding lakes except Lake Jake, from which it is separated by a pass shown as more than 700 feet (213 m.) higher than Lake Gale. We found evidence, which has been accepted, that Lake Gale discharged northward, over the present very slight alluvial saddle in Butte Valley, through pluvial Butte River (ca. 12 km. long) into Butte Bay of

Lake Franklin. The presence in both drainage basins of the relict dace, *Relictus solitarius*, confirms the connection.

Examination in 1942 of what we have taken to be the northern end of the drainage basin, and of the highest of the pluvial lake shorelines (fig. 49), seemed to leave little doubt regarding the discharge. About 5 km. north and 1 km. west of Stratton Ranch on the Elko–White Pine county line are two very minor spring sources less than 1 km. apart that discharge respectively south (Twin Springs) and north, on either side of a scarcely perceptible divide. About 1.5 km. farther north is the spring source of the northward-flowing Odgers Creek. Beginning less than 1 km. farther on, in the gently sloping valley, truncation and terracing of the lateral alluvial cones strongly suggest the major ancient water course of pluvial Butte River. The course extends down the narrow valley between approximated 6,300-foot (1,920-m.) contours as shown on the Elko 1: 250,000 map. The 6,282-foot (1,915-m.) altitude shown in the northern part of the bed of the lake, therefore indicates that here the lake must have been very shallow. In the southern basin, where the lake-bed altitude of 6,161 feet (1,878 m.) is shown, the greatest lake depth was presumably slightly less than the 150 feet (46 m.) entered by Snyder *et al.* Our approximation is 40 m. An alkaline lake must have persisted in the southern basin after the discharge failed. An elongate mountainous island 6 km. long is shown in the northern arm, as separated by a narrow channel at its north end, but we have no proof that the mountain was not a peninsula. Terraces at the base of a hillock just south of the mouth of Snow Creek fix the position of the shoreline there.

REMNANT WATERS.

The only live waters of consequence in this elongate basin seem to be confined to the northern arm. Snow and Paris creeks, arising in the highest parts of the Cherry Creek Range on the east side carry some water, mostly seasonally. There are a number of minor mountain springs, especially along the east and south sides of the south basin. The only waters that are known to or would be expected to support fish are the basin springs and their short outlets in the far north. We found these to comprise three groups, on the Wright and Stratton ranches, respectively on the north and south sides of the Elko and White Pine county line and on the Owens Ranch about 5 km. south of the line (fig. 49). Local testimony indicated that the discharges of these three groups are never connected. Twin Springs, about 6 km. north of the line, and barely on the Lake Gale side of the slight Franklin–Gale divide, were found to be nearly dry. Characteristics of the fish-inhabited springs are stated in the account of the habitat of *Relictus solitarius* (pp. 201–207).

The hydrography of this area has also been described and mapped by Glancy (1968).

REMNANT FISH LIFE.

The only native fish in the basin is the relict dace, *Relictus solitarius*, and it seems to be confined to the springs just mentioned, in the extreme north end of the trough. The Road Supervisor for White Pine County, Jerome Phalan Stratton, who had been reared in Butte Valley, told us on June 25, 1942, that all mountain springs in the area are fishless. An operator on the Stratton Ranch on the next day confirmed this testimony, and further stated that no fish occur in any of the mountain springs or mountain creeks of Butte Valley, that all of the valley springs in the basin contain "the same kind of minnow with no variation," and that carp occur through the valley (we took one in the spring creek on the Stratton Ranch and noted that planted trout also occurred there).

PLUVIAL LAKE WARING

Drainage basin in southeastern Elko County and northern White Pine County, Nevada (figs. 11, 13).

We recounted (Hubbs and Miller, 1948b, p. 54) the somewhat involved conceptions and

nomenclatural history of this major pluvial sump lake, for which we proposed the name pluvial Lake Waring. This name has been accepted by Snyder *et al.* (1964) and Feth (1964). This lake, like most others in the area, persists as an extensive alkaline flat that occasionally holds some water.

The greatly elongated drainage basin of Lake Waring, including that of the tributary Lake Steptoe, is bounded on the north tip and along the northern half of its eastern side by the Bonneville watershed; farther south, by the drainage basins of Lake Antelope, which was possibly tributary at its highest level, and of Lake Spring; at the south end by the basins of pluvial lakes Carpenter and Cave, which are physiographically part of or are related to the pluvial drainage of Colorado River; and on the west, from south to north, by the basins of pluvial White River and pluvial lakes Jake, Gale, Franklin, and Clover. This major north–south fault trough thus intervenes between the Columbia and Colorado river systems and bounds on the east the area of minor basins treated in this report, with the interpolation southward of the parallel trough of Spring Valley. The narrow drainage basin of Lake Waring extends almost due north from 38° 24′ to 41° 14′ N. lat., a distance of 263 km., whereas the greatest width was 60 km. and the average width only about 30 km.

The northern part of the basin (Goshute or Shafter Valley), which immediately surrounds the bed of Lake Waring, is bifurcate southward, where it extends on either side of the Dolly Varden Mountains. The eastern fork, for which we propose the name Antelope Bay, leads southward over a weak alluvial divide into the northern part of Antelope Valley (as usually mapped; Eakin, Maxey, and Robinson labelled the eastern part of the main basin "Antelope Valley"). The western fork connects through a divide floored with lava and alluvium into the tributary Steptoe Valley.

Pluvial Lake Waring largely filled its basin (exclusive of the drainage basins of lakes Steptoe and Antelope) and had the same bifurcate form, with the eastern fork wider than the western. The greatest length of the lake was about 96 km. North of the southern expansion the width reached 18 km. The western fork in a narrow extension reached almost to Currie and was probably separated by only 3 or 4 km. from the northern end of the tributary Lake Steptoe. The lake narrowly transgressed the lower part of the adjacent alluvial slopes. One small island rose in the northern part of the lake.

At its maximum depth of about 66 m., with highest water surface altitude (estimated by 2-foot altimeter) of about 5,760 feet (1,756 m.) and lowest point indicated on the lake bed of 5,545 feet (1,690 m.), Lake Waring covered 1,314 sq. km., which comprised 33 percent of the area (3,949 sq. km.) of its basin excluding the Steptoe basin (14 percent of the entire drainage area of 9,411 sq. km., including the Steptoe basin). The sharpness of the higher terraces indicates a high lake level for prolonged periods. A profuse water supply is understandable, since nearly all of the closely adjoining mountain crests on either side rise to altitudes above 2,100 m. and a considerable number of peaks rear to above 3,000 m. It is small wonder that Lake Waring so nearly filled its immediate basin, in view of the great volume of water that must have poured in through pluvial Steptoe River (including its dilation, pluvial Lake Steptoe). Large and prolonged flow is also indicated by the deep, sharp trench through the lava cross-barrier just above Currie, by which Lake Steptoe discharged into Lake Waring. As is noted below (p. 55), however, Lake Steptoe, according to our calculations, was very much smaller than has previously been indicated. Being smaller, Lake Steptoe must have lost less water through evaporation than it would have at a larger size; hence the contribution to the larger and presumably more permanent Lake Waring was greater.

There are no indications, either physiographic or faunistic, that pluvial Lake Waring discharged. As stated below, the lowest passes (through the eastern marginal mountains) are at least 40 m. higher than the highest beach lines. Some sub-

terranean outflow through one or more of these passes may, through stabilization of the lake level, have increased the sharpness of the higher terraces.

It is clear that pluvial Lake Steptoe overflowed directly into Lake Waring. In fact, Beckwith (1855) stated that Goshute Lake still so discharged during major floods (local testimony in 1938 and 1942, though consistently indicating ephemeral filling of the present Goshute Lake, was conflicting on this point). Whether Lake Antelope of Antelope Valley ever attained surface discharge into Antelope Bay of Lake Waring is doubtful (p. 60). There are no hints of other direct inflows, but a transfer of water and fish (*Relictus*) by distributary action across the alluvial divide between the Lake Franklin and Lake Waring basins, in one or both directions, seems highly probable (pp. 43–44).

LAKE WARING SHORELINE DATA.

Ancient shorelines, sharply retained along the lower slopes of the marginal bajadas of the great alkaline flat of Goshute Valley, furnish clear-cut evidence of high stands of pluvial Lake Waring.

The evidence of ancient lake levels is particularly striking where the rectified shorelines hinged on a lava nubbin on the east side of the valley 4.5 km. east-northeast of Shafter (location shown on fig. 12). The hillock was topped by Air Beacon 501, now shown as "Abandoned Beacon" on the Elko 1:250,000 map, just above the 5,700-foot (1,737-m.) interpolated contour. The longshore bars (fig. 9) were roughly charted here (by C.L.H.) on June 23, 1942, by using a hand compass and a 2-foot altimeter. The bars, largely bare or with low herbs, were composed of waveworn gravel and stones. All were elevated a few feet and were very regular and parallel. The clay soil of the intervening depressions supported deep-green sagebrush. As seen from the western side of the valley, shore features extend about halfway up toward the level of Silver Zone Pass.

The western alluvial slope opposite Shafter also was seen to be terraced (fig. 10) along the road

FIGURE 9. Bars on eastern shoreline in northern part of Lake Waring, between Shafter and Silver Zone Pass in White Pine County, Nevada; impinging on a lava nubbin. Elevations estimated by use of a 2-foot Paulin precision altimeter. From field sketch of June 23, 1942.

to Independence Valley, starting with a computed altitude of 1,698 m. on lacustrine clay at the foot of the alluvial slope, 7.6 km. west of Shafter. A particularly sharp terrace 0.5 km. farther west and 9 to 15 m. higher, with a deposit of wave-rounded gravel, indicated a long low-level stillstand. The even slope between estimated elevations of 1,739 and 1,751 m. showed traces of terraces. Obviously, the lake level was subject to much fluctuation. The slope above the definitive 1,760-m. top terrace was even, without further trace of shoreline features.

The terraces along the west shore are conspicuous and continuous from near Oasis, close to the extreme north end of the valley, almost to Currie, including the region south of Dolly Varden Siding on the Nevada Northern Railroad where the valley floor gently rises. In general, two well defined shorelines are evident toward the top level, a very sharp one near the base, and only one sharply distinct between. Southwest of Luke (north of Flowery Lake) we noticed a fine lake

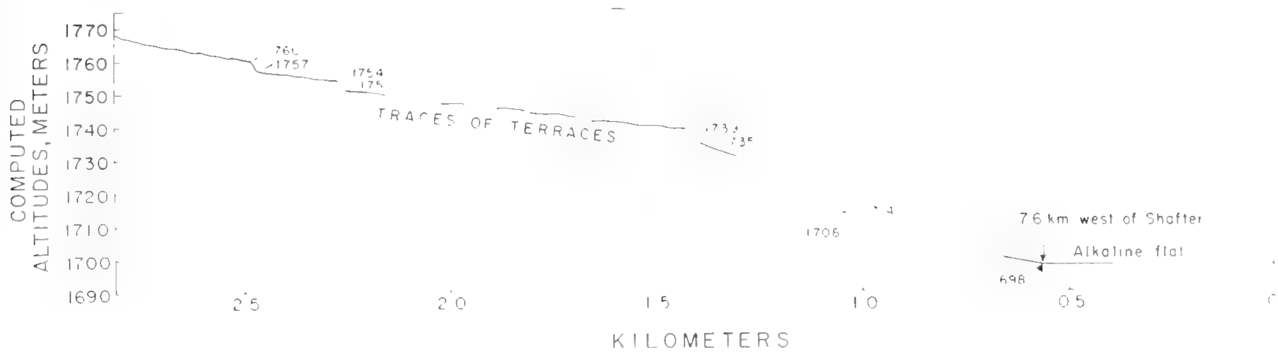


FIGURE 10. Shoreline terraces on bajada on west side of pluvial Lake Waring, west of Shafter, Elko County, Nevada. Sketched from quick survey on June 23, 1942. Elevations estimated by Paulin altimeter.

bar, and the 5,600-foot and 5,700-foot (1,707-m. and 1,737-m.) contours mapped in this region (on the Elko map) strongly suggest shoreline features. Various other evidences of the ancient lake were noted while travelling down the entire west side of the valley in 1942. The lake obviously extended to near the mouth of Phalan (not "Phalen") Creek 5 km. north of Currie. Whether the intervening distance was occupied by a narrow arm of the lake, at its highest level, or by the inlet river, is not yet clear,

The position of the higher lake shores in the southern part of pluvial Antelope Bay is indicated, from notations and sketches made on June 24, 1942, to be about the same as to the northward. At the north tip of Kingsley Mountains, immediately north of and parallel to the road toward Ibapah, Utah, two low terraces parallel the road where it skirts a lava nubbin 7.4 km. from U. S. Highway 50, and a sharp, even bar, made up of beach-worn stones, conjoins the road 5.3 km. from U. S. Highway 50, for about 2 km. Close to the highway a minor terrace runs along the road and two more run parallel, just to the southwest. The alluvial slope rising toward the southwest showed no signs of terracing. About 5 km. northwest of the highway, near where a corral and spring are shown on the Elko map, clear-cut terraces were seen on low hills. These beach features appear, by use of this map, to lie between the 5,700-foot (1,737-m.) and 5,800-foot (1,768-m.) contours. While following the structural trough between the beds of lakes Waring and Antelope in 1942, it was concluded that Antelope Bay pinched out not far from the Elko-White Pine county line. This observation, using the same chart, again places the high lake levels between the 5,700-foot and 5,800-foot contours. The stippled area on the map looks deceivingly like a lake bed, but is crossed by the two contours just mentioned and obviously portrays sloping, sandy, alluvial or eolian, deposits—like those shown on the same map to the westward, in the Lake Steptoe basin (p. 56). Our mapping of Antelope Bay of Lake Waring essentially agrees with the highest recognized Pleistocene lake level mapped by Harrill (1971).

Everywhere around the basin the passes seem to be definitely higher than any discernible shoreline (estimated at about 1,756 m.). The lowest point is probably Silver Zone Pass, shown between the 5,800-foot (1,768-m.) and 6,000-foot (1,829-m.) contours on the Elko map. This pass cuts through the Toana Range, on the Waring-Bonneville divide. The very flat pass at Cobre, just beyond the north end of the basin, on the same watershed divide, is shown on the same map to top where the 5,900-foot (1,798-m.) contours are very slightly separated. The map shows the 6,000-foot (1,829-m.) contours barely separated at White Horse Pass, through the Goshute Mountains, also on the same basin divide. All the other passes are definitely higher at the south end, and the Steptoe–Carpenter divide is shown as

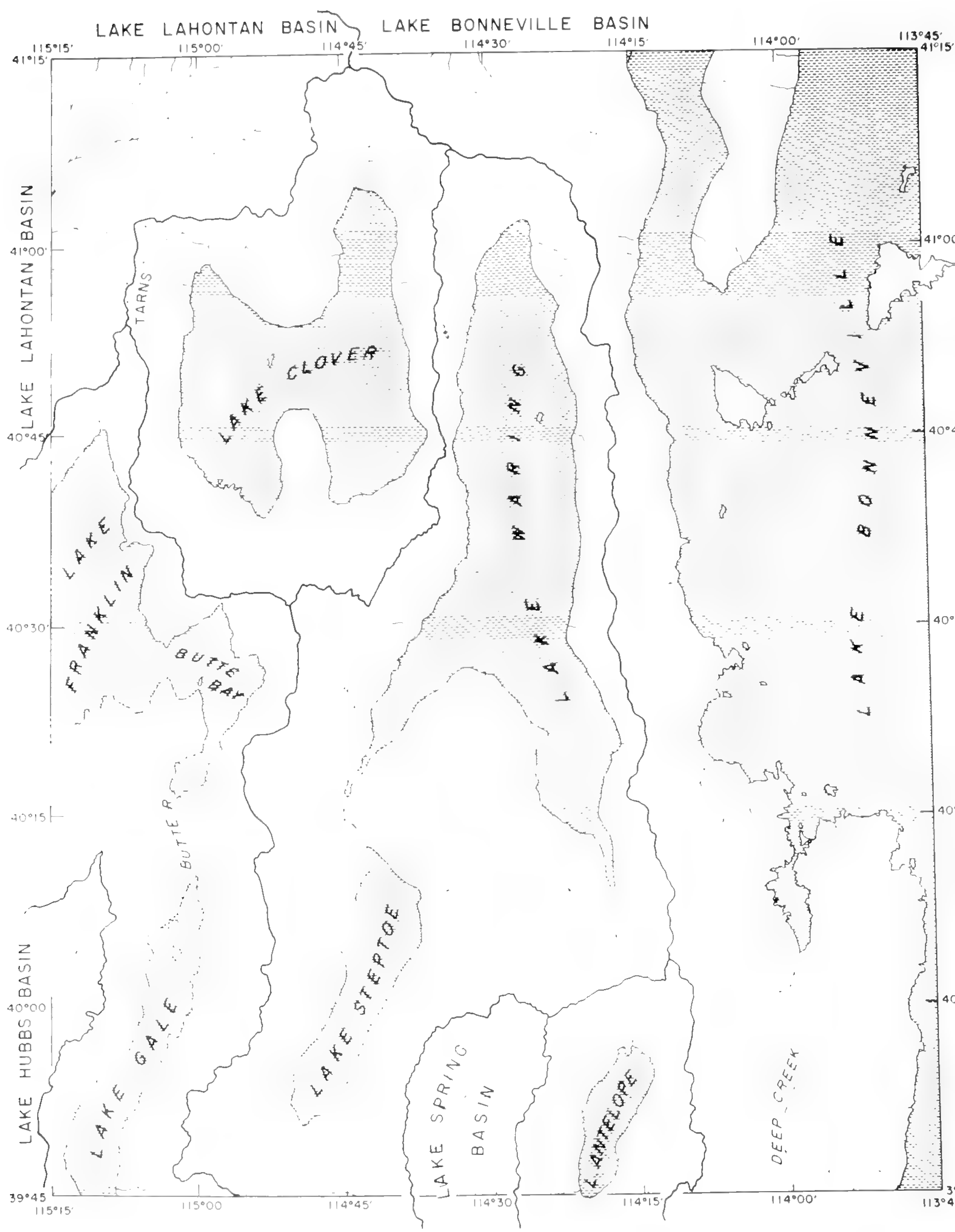


FIGURE 11. Detail of pluvial hydrography of northeastern part of study area ('A' on fig. 1).

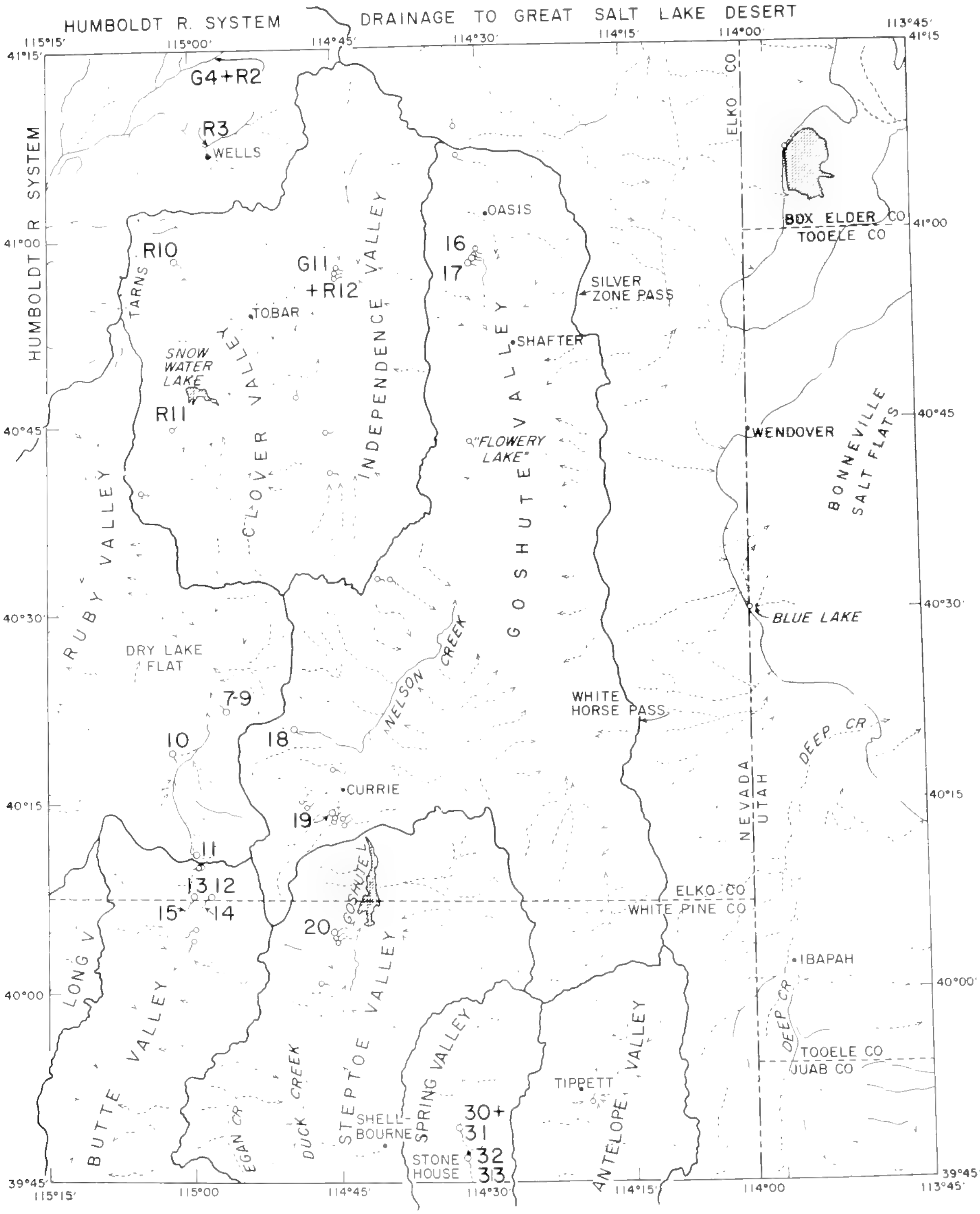


FIGURE 12. Detail of modern hydrography of northeastern part of study area ('A' on fig. 1); showing also key geographic features. Locations for *Gila* (G–) and *Rhinichthys* (R–), and Collections for *Relictus* (–).

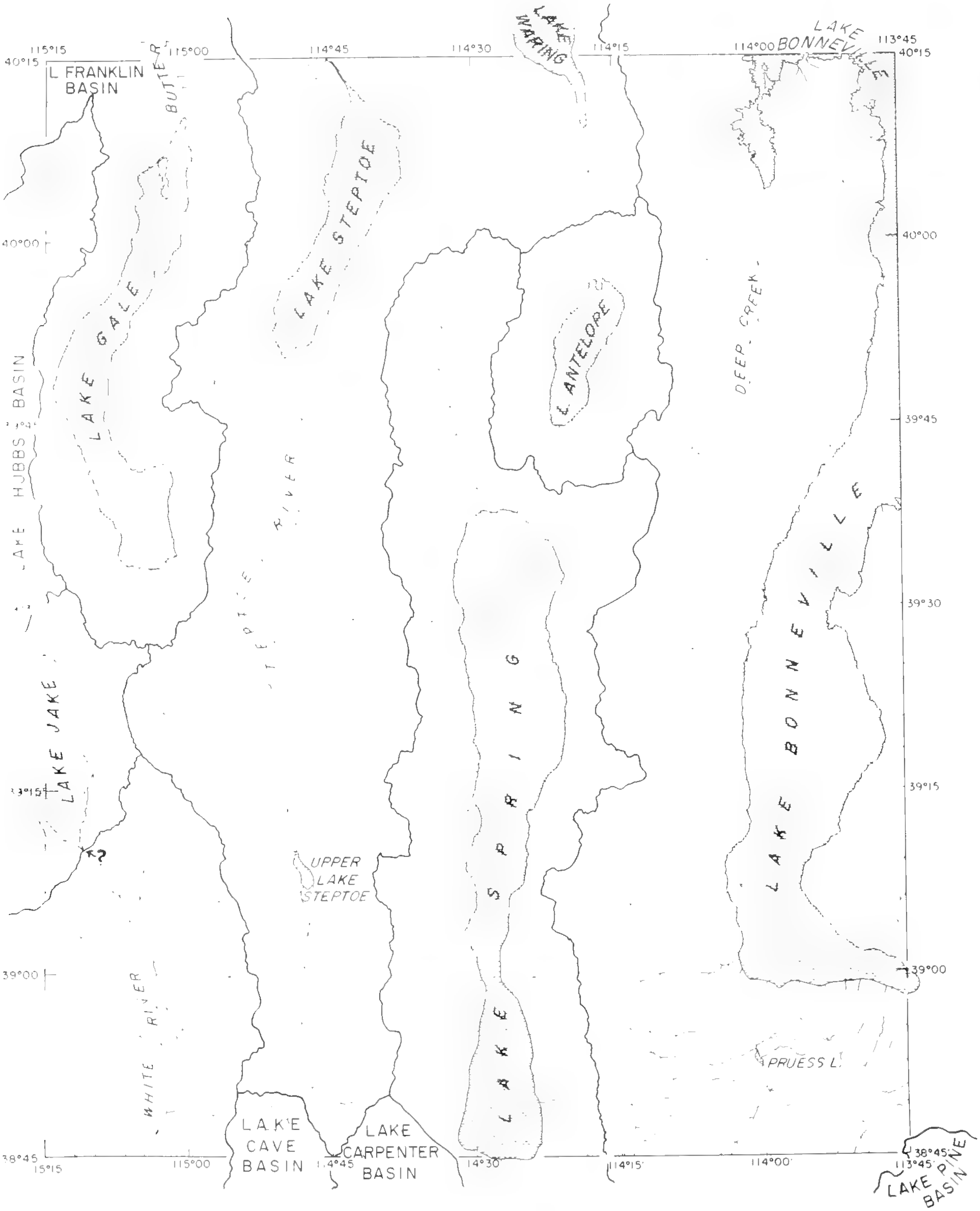


FIGURE 13. Detail of pluvial hydrography of southeastern part of study area ('B' on fig. 1).

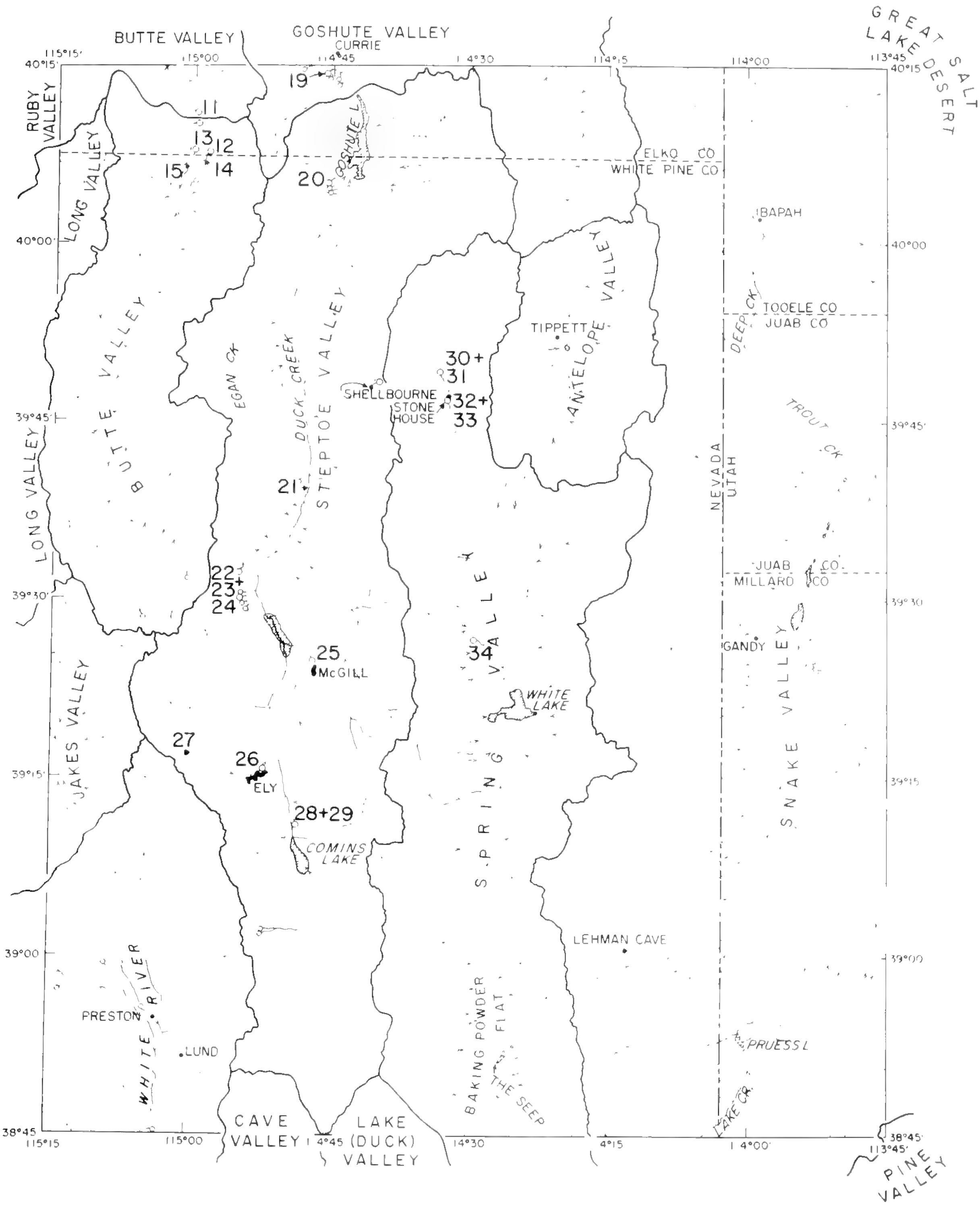


FIGURE 14. Detail of modern hydrography of southeastern part of study area ('B' on fig. 1): showing also key geographic features and Collections for *Relictus* (–).

higher than 7,200 feet (2,195 m.). Thus, physiographically, the Waring drainage basin is most closely related to that of Lake Bonneville, but there is no hydrographical or ichthyological basis for postulating any past surface-water connection in that direction.

Remnant Waters.

In view of the tremendous water storage in pluvial time and the height of the almost completely margining mountains, it is no wonder that the drainage basin of Lake Waring is not completely desiccated. Most of the surface waters are in Steptoe Valley (these are discussed below, under the heading of Lake Steptoe). The connected and possibly once tributary basin (Antelope Valley) of pluvial Lake Antelope (pp. 60–61) is now almost completely dry.

Goshute Valley, which was so largely filled with pluvial water, now stands almost completely parched. On rare occasions, as during our visit in June, 1942, much of the great alkaline flat is shallowly and briefly covered with water. The single, small perennial stream in the basin, Phalan Creek, the outlet of Twin Springs on the Phalan Ranch, flows eastward to the south end of the old lake bed, which it traverses for a considerable distance northeastward, as Nelson Creek. All other tributaries are short and/or intermittent. The hydrography of Goshute Valley (as here interpreted) was treated by Eakin, Maxey, and Robinson, 1951).

There are very few springs in the drainage basin north of Steptoe Valley proper. Twin Springs, just mentioned, emerge from a major bajada, at an altitude of 6,200 feet (1,890 m.) according to the Elko map. A group of springs near the junction of McDermitt Creek and the ancient outlet channel from Lake Steptoe, about 3 to 4.5 km. above (south of) Currie, is ditched to that town. The only extensive group of springs around the former margin of Lake Waring are those on Johnson Ranch on the west side near the north end, about 7 km. south of Oasis. They lie near the old beach line, one on the alluvial slope and others in a meadow (as described on p. 203). According to local testimony, the combined waste water may run as far as 10 to 16 km., entrenched in the old lake bed. The only other spring on or adjacent to the lake bed forms what is mapped as "Flowery Lake" (known locally as "Flower Lake"), toward the western side of the main body of the ancient lake. On June 21, 1942, this "lake" was found to be a springfed pool 18 m. long, 0.3 m. deep, and largely choked with vegetation; about 0.4 km. north was a chain of small mound springs forming a marshy area about 0.15 km. across (p. 202). There are extremely few small springs in the margining mountains. Boone Springs in Boone Canyon, tributary to the basin of the eastern arm of Lake Waring at an elevation of about 6,300 feet (1,920 m.) irrigated 2 or 3 acres of meadow in 1942 and was presumably fishless. Other springs with the same name, in the southern part of the Pequop Mountains (on the west side of the basin), were not visited, but like most mountain springs are presumably fishless.

These traces of water in Goshute Valley are a pitiful remnant of the vast pluvial lake that so nearly filled the basin. Presumably the high Ruby–East Humboldt Range and other mountains to the westward have cast a rain shadow on Goshute Valley.

Fish Life.

As we have already indicated (Hubbs and Miller, 1948b, pp. 53–55), the remnant waters of this drainage basin, along with that of lakes Franklin and Gale, are populated by a single, sharply distinct, native species of fish (herein treated as *Relictus solitarius*, pp. 196–226). We believe that its original distribution was in springs and streams once tributary either to pluvial lakes Waring and Steptoe or to pluvial lakes Franklin and Gale, and that it was transferred across an intervening alluvial fan by distributary stream flow (p. 43). There is no evidence, however, and it now seems highly improbable, that the

fish may be a relict dating from some very ancient stream system that has become disrupted into the two pluvial drainage basins.

Relictus solitarius now seems to be limited in the great sump basin of Goshute Valley to the three habitable groups of springs, those just above Currie and those on the Phalan and Johnson ranches. In addition, as indicated below, it occupies many springs and rivulets in the tributary Steptoe Valley. No exotic fishes were taken in the springs of Goshute Valley, except for rainbow and brook trout near Currie. Several exotics have become established in the springs and creeks of Steptoe Valley (pp. 236–240).

Pluvial Lake Steptoe

Drainage basin in southeastern Elko and northeastern White Pine counties, eastern Nevada (figs. 7, 11, 13).

Pleistocene Lake Steptoe, which was named "Lower Steptoe Lake" by Clark and Riddell (1920, p. 19), and has generally been termed Lake Steptoe, is now represented by the ephemeral Goshute Lake, in Steptoe Valley above the narrows just south of Currie. This playa sump straddles the Elko-White Pine county line. It occupies the lowest, northern end of Steptoe Valley (in some usages of that name; many residents consulted applied the name also to the large semi-detached Goshute Valley, the site of pluvial Lake Waring, that extends northward nearly to Cobre, or at least the southwestern part of that valley). Others called the basin of Lake Waring "Shafter Valley" and this nomenclature appears on some maps. Other maps, including the 1958 edition of the Elko 1:250,000 map, extend the name Steptoe through the intervening narrows, but not into Goshute Valley. The 1965 edition of the same map and the U. S. G. S. map of the State of Nevada (1965) carry the label "Steptoe Valley" across the whole basin from near Currie to near Shafter, and restrict "Goshute Valley" to the contiguous, extreme north end of the graben, between Shafter and Oasis. However, Eakin *et al.* (1967) in the state of Nevada water-resources appraisal of Steptoe Valley, held that this valley "extends northward from the southern end of White Pine County for about 110 miles into the southern part of Elko County," and mapped the end of the basin at the covergence of the geologic contacts, about 10 km. within the hydrographic basin of what we term Goshute Valley. Gibbes' 1873 map (p. 8) labels the main basin "Goshute Desert."

Steptoe and Waring basins are part of a greatly elongated trough that extends farther southward in Cave Valley, the site of a third pluvial lake, Lake Cave, which appears to be structurally related most closely to the Colorado River drainage basin. Early conceptions regarding Lake Steptoe, in part erroneous, and its relation to other pluvial lakes, have been recounted by us (Hubbs and Miller, 1948b, p. 54).

The drainage basin of Lake Steptoe is bounded on the north by that of Lake Waring, to which it was tributary; on the east by that of Lake Antelope (a semidisjunct part of Goshute Valley) and that of Lake Spring (Antelope and Spring valleys completely separate the Steptoe and Bonneville watersheds). On the short southeastern and southwestern sectors, the drainage divide is common with the watersheds of Lake and Cave valleys, the sites of Pleistocene lakes Carpenter and Cave, respectively. Those lakes were tributary to, or disjunct from, the Colorado River basin. Beyond the divide on the west side, from south to north, the drainage is toward the White River (tributary to Colorado River in pluvial time), Jakes Valley (Lake Jake), and Butte Valley (lakes Gale and Franklin).

The Steptoe drainage basin, as we interpret it, extends almost due north–south, and is almost four times as long (163 km.) as its greatest width. Over most of its length the width is relatively uniform, but varies from 18.5 to 45 km.

In our present view, Lake Steptoe could not have been nearly as large as it was mapped by Clark and Riddell (1920), by us (1948b, pp. 53–55, lake no. 27), by Snyder *et al.* (1964, lake

no. 99), and by others. The two older of these maps, which were drawn prior to the topographic mapping, exaggerate the outline much as does the 1964 map, on which the outline roughly follows the 6,100-foot (1,859-m.) contour as delineated on the Ely and Lund 1:250,000 maps, but with fluctuations from 6,000 to 6,600 feet. The 1964 map, however, carries the lake beyond the crest of the Steptoe-Waring divide, to put the source of the outlet channel 8 km. north-northwest of Currie, instead of its actual position 2.5 km. south of that town. In so doing, the lake margin when redrafted onto the Elko map is seen to intersect contours ranging from 6,100 to 6,600 feet (1,859 to 2,012 m.). The outlet channel according to that precise map is between the 5,900-foot (1,798-m.) and 5,800-foot (1,768-m.) contours. When the lake is charted at a little below the 5,900-foot contour, which on other grounds we think it approximately reached, its straight-line length is indicated to have been only 42 km., in contrast to the 110 km. derived from the published maps (as measured on the 1964 map). The impossibility of even a 6,100-foot lake level is obvious when we note that the altitude of Silver Zone Pass, between the Waring and Bonneville drainage basins, is indicated as being between 5,800 and 6,000 feet.

Furthermore, Snyder *et al.* attributed to Lake Steptoe the wholly implausible depth of 350 feet. Both the outlet channel and the bed of the always very shallow, tributary, ephemeral present Lake Goshute are mapped as lying between the contours of 5,800 and 5,900 feet, and we feel sure from our field reconnaissance that the difference in elevation is considerably less than 100 feet (30 m.).

Sand deposits extending eastward from Goshute Lake, then radiating into canyons (represented by a stippled area on the Elko map) may have suggested to Clark and Riddell and others a lake bed, but the area is crossed by the 5,900- and 6,000-foot contours and extends to the 6,200-foot line. Indeed, Clark and Riddell (1920, pl. 2) mapped an "Old beach" margining the area, and we suppose that this erroneous mapping led to the misconception of the lake size. This area apparently represents an aggradation of sand, transported either by wind or water, or by both. A similar but smaller area to the east extends along the axis of the northern segment of Antelope Valley (p. 49).

The lake itself, as we now interpret it, measured 42 km. in length and 10 km. in greatest width. These dimensions are far under those stated by Clark and Riddell (1920, p. 20), "over 30 miles [48 km.] long and 11½ miles [19 km.] wide," though they mapped the Pleistocene lake bed (on pl. 1) as about 60 miles (97 km.) long, as it would be if the lake reached the "Old beach line" charted on their plate 2. The area of the lake is now computed as 282 sq. km., or 6 percent of the area (4,646 sq. km.) of its drainage basin. This is much less than the average percentage for the basins under treatment, and only about one-third that for the entire Lake Waring watershed, including the Steptoe portion. The obvious explanation for this exception is that Lake Steptoe drained into Lake Waring, which we now know was very much larger and deeper, though it lay in a basin that is now much the more arid, and presumably also was during the pluvial. Had it not been for the discharge, Lake Steptoe would no doubt have been much longer and deeper, for it is closely and almost completely hemmed in by mountains mostly rising to altitudes higher than 2,500 m., and attaining elevations higher than 3,000 m. in several peaks, in both the Schell Creek and Egan ranges.

Because Lake Steptoe was much shorter than it has commonly been thought to have been, the lengthwise pluvial Steptoe River, as we have called it (Hubbs and Miller, 1948b, p. 54), was correspondingly longer than previously indicated. At the height of the late pluvial it was no doubt a major stream.

It has been observed, by us and others, that shoreline remnants are relatively inconspicuous in Steptoe Valley. The probable reason is that the lake, because of the altitude of its discharge chan-

nel, did not rise far onto the gentle slopes of the valley floor, and the marginal shoals were in all probability so well protected against wave action by a heavy growth of marsh vegetation that sharp terraces or bars were not formed. Within a single depression, for example that of Lake LeConte in the Salton Sea basin of southeastern California, we have found that the boldness of shoreline features on steep slopes contrasts very sharply with their almost complete absence on very slight slopes.

Since all passes in the rim of the basin of Lake Steptoe, except the outlet into Goshute Valley, are indicated by the Elko, Ely, and Lund 1:250,000 maps to be more than 200 m. higher than Lake Steptoe as now delineated, and since there are no indications that any of the lakes in adjoining basins rose high enough to crest the divide (indeed all of them drained or would have drained elsewhere), there was no inflow, at least of surface water, from any of the surrounding depressed basins. In this conclusion, we disregard pluvial Upper Lake Steptoe (p. 59), which merely lay in the course of pluvial Steptoe River, and the lake (no. 27) that Snyder *et al.* (1964) indicated as of Pleistocene occurrence in Egan Creek Valley, but which we think could not have existed there, at least in late Pleistocene time (p. 58).

There is clear evidence of the discharge of pluvial Lake Steptoe, between the north end of the present Steptoe sump (Goshute Lake) and Currie (a straight-line distance of about 7 km.). Examination of this area on August 24 and 25, 1938, and also in 1934 and 1942, disclosed a definite stream channel, steeply entrenched in bedrock about 2 to 3 km. south of (above) Currie, that served as the course of the Nevada Northern Railroad (Hubbs and Miller, 1948b, p. 54). It appears that the large alluvial cone formed by McDermitt Creek and smaller draws, from the west, had in past time, probably early pluvial, blocked a former outlet channel, so as to force the stream onto bedrock, which was then entrenched. Rejuvenated erosion extended up McDermitt Creek, to leave the rather strong lateral terraces that are visible there. The lateral alluvial cones were truncated by the outlet of Lake Steptoe. A now dry river channel that is obvious from Currie to the mouth of Phalan Creek (about 6 km.) probably formed after Lake Waring dropped below its highest level to lay bare the bottom of the narrow north-end tongue of the basin. The Elko map shows the 5,800-foot (1,768-m.) contour extending as a V into the outlet channel to about 2.5 km. south of Currie, but the interpolated 5,900-foot (1,798-m.) contours are separated throughout.

REMNANT WATERS.

Lake Steptoe is represented by the remnant sump, Goshute Lake; by an axial, more or less continuous tributary thereto; by a number of other small, mountain and valley streamlets; and by many springs.

As already mentioned, Goshute Lake is an ephemeral body of water at the extreme north end of the basin of pluvial Lake Steptoe. It is shown on the Elko map as narrow and 13.5 km. long, with a marshy extension southward, fed by Duck Creek and lateral streamlets.

The main axial stream in this valley, the remnant of pluvial Steptoe River, usually carries some water, even in dry seasons, despite the use of most of the available water by the mills at McGill, as Clark and Riddell (1920) noted long ago in describing the streams and springs of the valley. About a century ago explorers reported that this stream required bridging for wagons to pass, though it was said to go dry later in the season. The stream is labelled Duck Creek on most maps, though locally we found it usually called "Steptoe Slough." On the Ely 1:250,000 map (1959) it is labelled Duck Creek on its lower half, then Murray Creek just below Ely. It is labelled Steptoe Creek just above that town, and along the watercourse that debauches from the Schell Creek Range and flows westward to join the axial stream course at a right angle. Then, farther south, above a marsh just south of the abrupt bend in "Steptoe

Creek," the axial stream is again labelled Murray Creek on the map. However, the Ely 15-minute Quadrangle labels the axial stream Willow Creek below the point where Willow Creek proper joins the axial course at a right angle. All the axial courses, however named, we regard as remnants of pluvial Steptoe River. Except during torrential precipitation the streams on the valley floor are mostly small and slow. There are also a considerable number of more or less permanent streams, in the canyons of the adjacent mountains, that are devoid of native fish.

In addition to numerous mountain springs, a number of valley springs extend from 92 km. north to 10 km. southeast of Ely; these locations range from 18 km. south of the north end of the basin to 48 km. north of the south end. From north to south the main valley springwaters are:

Springs on the Elko County side of the Elko–White Pine county line.

Springs on the Cardano Ranch, feeding the marshes just south of Goshute Lake, and minor springs in the same general region, all on the west side.

After a long gap (nearly 40 km.), Monte Neva Hot Springs ("Melvin Hot Springs" of Clark and Riddell, 1920), with cooler outflow below.

Springs on the Campbell or Steptoe Ranch, and, just beyond, Grass Springs, with many minor springs in file, issuing along a probable fault line in what Clark and Riddell (1920) and Eakin *et al.* (1967) called the "Campbell Embayment."

Springs on Dairy Ranch near McGill, the first from the north on the east side of the valley.

Spring water at Georgetown Ranch, near Ely.

Finally, springs on the CCC (Consolidated Copper Company), now C–B Ranch, in mid-valley, where Steptoe Creek turns abruptly northward on its alluvial fan.

Farther south, in the part of the basin that discharged through Upper Steptoe Lake, isolated mountain springs and a cluster of cool outflows in Willow Creek Basin—all seemingly devoid of native fish (p. 60).

All of these spring waters are discussed in more detail in the account of the habitat of *Relictus solitarius* (pp. 204–206). The hydrography of Steptoe Valley has been treated by Eakin *et al.* (1967).

Fish Life.

The only native fish in this drainage, as also in the watersheds of lakes Waring, Gale, and Franklin, is the relict dace, *Relictus solitarius*. It occurs, usually in great abundance, almost entirely in the warmish (neither hot nor cold) valley springs and in the springfed valley creeks and sloughs. The mountain springs and creeks seem to be avoided by native fishes. The only seemingly suitable spring waters where we failed to find this fish are those on the Murphy, formerly Dolan, Ranch on the Elko County side of the Elko–White Pine county line. Here, and in marsh below, it probably once abounded, according to local testimony (p. 206), but it is now replaced by the obviously introduced Utah chub, *Gila atraria* (p. 231). Other introduced fish found in the basin are rainbow and brook trout, carp, goldfish, carp × goldfish hybrids, and Sacramento perch (pp. 235–240).

The Supposed Lake in Egan Basin.

A second lake (no. 27) tributary to Steptoe Valley was indicated by Snyder *et al.* (1964), followed by Morrison (1965, fig. 1), to have existed in the nearly enclosed Egan Basin. That basin lies just west of the mid-length of the Lake Steptoe bed, between the narrow northern end of the Egan Range and the southern end of the Cherry Creek Mountains, with a relatively low pass extending southward to the southern basin of Butte Valley, that is, toward what was the deepest part of pluvial Lake Gale. The lake has not been named, but was listed by Snyder *et al.* as having had an area of 10 square miles in a drainage basin of 62 square miles. However, the topographic features, as shown on the Ely 1:250,000 map, provide little basis for the hypothesis that a pluvial lake existed in this basin. The lake as mapped extended to just within (below) the 6,800-foot (2,073-m.) contour and covered the 6,600-foot (2,012-m.) and 6,400-foot (1,951-m.) contours, both of which passed without closing through the very narrow and steep outlet canyon

of Egan Creek, into which canyon the 6,200-foot (1,890-m.) contour inserts from Steptoe Valley.

Any ponding of water in this basin that could have occurred would necessarily have been prior to the deep erosion of the canyon, presumably during an erosional epoch that preceded the late pluvial period with which we are concerned. We question whether any lake ever existed here, but have made no pertinent field studies. The hydrology of Egan Creek was briefly described by Clark and Riddell (1920, p. 34). The canyon was traversed by the old Overland Mail Route (p. 235).

Pluvial Upper Lake Steptoe

Drainage basin comprising the southernmost fifth of Steptoe Valley, in south-central White Pine County, eastern Nevada (fig. 13).

Clark and Riddell (1920, p. 20) briefly indicated that a small and shallow "ancient lake" accumulated in this area, and they assigned to it a definitive name, "Upper Steptoe Lake," to distinguish it from the main "ancient lake" of the basin, which they named "Lower Steptoe Lake." We (1948b, pp. 54–55, map 1) mapped but did not name or discuss the southern 'lake.' Snyder *et al.* (1964) mapped the lake (their no. 100) as Pleistocene, but indicated it as unnamed (despite Clark and Riddell's proposal). Snyder *et al.* designated the lake area as 10 square miles (26 sq. km.) and the drainage-basin area as 358 square miles (927 sq. km.), and stated that it drained into Lake Steptoe (an obvious conclusion). Our estimates are 13 sq. km. for the lake area (not precise), less than 2 percent of the area, 816 sq. km., of the drainage basin.

We provisionally and rather doubtfully include the lake as of Pleistocene age, and name it, in slight emendation, Upper Lake Steptoe, reserving the unmodified name Lake Steptoe for the larger and more definite impoundment to the north.

As Clark and Riddell indicated, it appears that the "ancient lake"—and this would seem to be true, even though it was merely a pond, or even a marsh—accumulated above the narrows in the valley, where the axial drainage was slightly blocked by alluvial aggradation from the upper segment of Steptoe Creek on the east side and Sawmill Creek on the west side. These authors logically added that "the lake was apparently drained by the dissecting of this alluvial divide."

We fail to see how a lake of considerable depth and size could have accumulated here, at least in late pluvial time. However, the evidence of a cross-basin barrier suggests that the extensive meadows may represent the silted-in remnant of an ancient lake, of shallow depth and about 10 km. long by about 3 km. in greatest width. The maximum primary dimensions of the drainage basin are 23 × 48 km. The lake and basin are shown on the Ely 1:250,000 map, the Ely 15-minute Quadrangle, and the Comins Lake 7.5-minute Quadrangle.

Remnant Waters.

The ancient lake is represented, we think largely by reason of earthen impoundments, by a variable body of water extending about 1 km. regularly, and about 2 km. rarely, southward from near the abrupt northward turn of Steptoe Creek, as is shown on Clark and Riddell's map (1920, pl. 2) and on the quadrangles mentioned above. According to local information, the southern, intermittent area filled in 1969, as a result of unusually heavy snow and rain, for the first time for 35 years. The highway embankment was about 3 m. higher than the small, cutoff northern piece of the main pond. No shoreline indications of a pluvial lake were seen.

The modern lake was named Cummings Lake by Clark and Riddell (1920), who also dealt with Cummings Ranch and Cummings Spring, north of Ely in the same valley. The Ely 15-minute Quadrangle (1958) uses the name Comins Lake, as does the Comins Lake 7.5-minute Quadrangle; the U.S.G.S. State of Nevada map, 1:500,000 (1965) gives the name Comins Meadow to the area just south of the modern lake (unnamed). Local testimony seemed to indicate

the spelling of Cummins or Cumin Lake. We assume that Comins is the correct spelling, for we note that the History of Nevada, edited by Myron Angel (1881), provided a biographical sketch and figure of Hon. Henry A. Comins, who settled in Nevada in 1863, removed to White Pine [County] in 1869, and engaged in lumbering, farming, and mining.

The two streams of the drainage basin, both in part permanent, arise in the Egan Range. The main one, Willow Creek, which rises in the profusely spring-fed, relatively broad and flat Willow Creek Basin, on the eastern slope of the range, near the north border of Sec. 35, T. 14 N., R. 63 E., irrigates Willow Ranch, and contributes some flow to the valley axis, but becomes intermittent above Comins Lake. Farther south, Willow Creek is paralleled in its eastward flow by Williams Creek, which is intermittent in the valley.

Fish Life.

No trace of native fish was found in the drainage basin by a reconnaissance on August 16–17, 1969, although *Relictus* abounds in Fish Pond Springs immediately below, in the bend of Steptoe Creek (Collections 28 and 29). Spring-fed Willow Creek appeared from an inspection of the maps to be a propitious site for *Relictus*, but the springs and their outflow were found to be inhabited only by introduced trout. The inspection disclosed no apparently suitable habitat for the relict dace, which ordinarily avoids cold springs and mountain streams.

Comins Lake was found, unexpectedly, to swarm with the Utah chub, *Gila atraria*, obviously as a result of a recent, previously unreported introduction (pp. 231–232).

Local testimony indicated that trout and bass (presumably *Micropterus salmoides*) were stocked in Comins Lake in the spring of 1969.

Pluvial Lake Antelope

Drainage basin in northeastern corner of White Pine County, eastern Nevada (figs. 11, 13).

This minor pluvial lake was named by Jones (1940) and the confused history of its drainage relations were recounted by us (Hubbs and Miller, 1948b, pp. 55–56). The situation is now considerably clarified by use of the Ely 1:250,000 map. The lake undoubtedly occupied a separate fault-block depression, though it lies in the trough, long known throughout as Antelope Valley, that continues into or even beyond the southeastern fork of the Lake Waring basin. The Lake Antelope basin has been mapped as Tippett Valley by Harrill (1971) and by Rush *et al.* (1971). The saddle that splits the drainage that in pluvial time flowed northward into Antelope Bay of Lake Waring (p. 49) and southward into Lake Antelope, is attributable not only to the close approximation of the slopes of the Goshute Mountains and the Antelope Range, but also to the development of a major alluvial fan from the main stream course in the Antelope Range. The fan is delineated on the Ely map by ditches radiating downward to supply both watersheds.

The pluvial-lake drainage basins surrounding the Lake Antelope basin are Waring to the north, Bonneville to the east, and Spring to the south and west (just missing near-contact with any headwaters to Lake Steptoe).

The roughly oblong drainage basin measures 47 km. long by 27 km. in greatest width. The corresponding dimensions of the centrally located lake were probably 23 and 7 km. The lake bed is deepest near the middle, where a pond accumulates (Elko 1:250,000 map).

As we have sketched it, largely on the basis of field reconnaissance (C.L.H.) of June 24, 1942, and on an examination of the Pleistocene lake map of Snyder *et al.* (1964), Lake Antelope covered at its highest stage 125 sq. km., or 14 percent of the area (870 sq. km.) of its drainage basin. Its greatest depth was estimated by those authors to have been 75 feet (23 m.). Its outline seems to have run slightly above the 5,700-foot (1,737-m.) interpolated contour on the Ely 1:250,000 map. The rough correspondence with the maximum height of Lake Waring, in the same

structural trough, elicits the thought that the two pluvial lakes may have had an underground connection through an alluvial block, or possibly that the waters were confluent and that the alluvial aggradation was postpluvial.

Oddly, the rather flat mountain passes between the pluvial basins of Lake Antelope and Lake Waring, between Lake Antelope and Lake Bonneville, and between Lake Waring and Lake Bonneville, are all mapped as cresting between the 5,800-foot (1,768-m.) and 6,000-foot (1,829-m.) contours (as drawn on the Elko 1:250,000 map). When these passes were all checked in 1942, no indication was found of any surface-water pluvial discharge. The approximate agreement in pass altitudes renders almost hopeless any attempt to reconstruct any possible remote-pluvial drainage pattern.

The 1942 field reconnaissance, taken on the old Overland Mail Route, indicated that definite shorelines persist around the outlines of pluvial Lake Antelope. The field record provided material for the following revised description of shore features, in order of observation:

0.0 km.: Approaching on the road from Deep Creek (Ibapah), arrived between two beach lines about 6 m. apart in elevation and about 0.15 km. on either side of the road [these beaches presumably lie on the gently curved ridge, followed by the road, shown below the 5,700-foot (1,737-m.) contour on the Elko map]. Below, on the lake flat, are rather large dunes.

2.9 km.: On definite terrace 43 m. below Antelope–Bonneville divide (by altimeter, not rechecked); some standing water on the lake sump.

3.7 km.: Bench extended from mountain onto flat as a definite though somewhat complex bar, which ran 2.7 km. before merging with bajada from Antelope Range. This bar was separated from mountains along its course by a lower flat, in places as wide as 1.5 km.; from which flat, drainage had broken through the bar in two places. Water-worn stones were found on the bar where it was followed by the road.

7.2 km.: Junction with road down Antelope Valley from north; beach lines observed just to north.

12.4 km.: Arrived at Tippett (49 m. below Antelope–Bonneville divide by altimeter; not rechecked).

13.7 km.: About 7 m. below distinct wave-cut terrace, truncating alluvial cones.

18.2 km.: Near end of sand dunes.

These observations seem consistent with the mapping of the lake and its drainage basin by Snyder *et al.* (1964) and by Harrill (1971). Some features shown on the Ely 1:250,000 map presumably represent bars and dunes.

Remnant Waters and Apparent Lack of Fish.

Throughout Antelope Valley, both north and south of the divide that separated the drainages into lakes Waring and Antelope, we saw no springs that could possibly be expected to harbor fish. The region about Tippett is irrigated by water piped and ditched from a warm spring in the Antelope Range, but we saw no fish in the ditches. This was reputed to be the only permanent water source in the basin.

Local informers, familiar with native creek fishes in Deep Creek (in the drainage basin of Lake Bonneville, just beyond the intervening divide), stated that no fish occur in the Tippett area. In all probability there are none, and none may have occurred even when the pluvial lake filled the lower part of the basin during late Pleistocene time. At an earlier pluvial period lakes Antelope and Waring were possibly connected, and fish then may have occurred in the Lake Antelope basin.

PLUVIAL LAKE SPRING (SEPARATED BY LOW DIVIDES FROM BOTH BONNEVILLE AND COLORADO SYSTEMS)

One trenchlike depressed basin that included a pluvial lake, namely that of Lake Spring, may represent an ancient disruption of either the Bonneville basin or the pluvial Carpenter River, and

hence also the White River division, of the Colorado River drainage system. Unfortunately, it seems not to have retained any native fish fauna, for any such remnant would almost surely have provided a clue to the past hydrographic connections.

Drainage basin extending through nearly all of the north-south extent of eastern White Pine County and into northeastern Lincoln County, in far-eastern Nevada (figs. 11, 13).

This lake was named by Jones (1940) and was briefly discussed by us (1948b, pp. 56–57). Its floor is a long, flat valley, with a major, occasionally dry, sump locally called White Lake, north of the middle of the basin. At the south end is the narrowly connected Baking Powder Flat, containing "The Seep."

The basin of Lake Spring is bounded on the north end by the drainage of Lake Steptoe; on the east side, by the watersheds of lakes Antelope and Bonneville; at the extreme south end and part way up the west side, by the tributaries of Lake Carpenter; throughout the rest of the west side by the drainage basin of Lake Steptoe. The basin of Lake Spring thus intervenes between the major hydrographic systems of Lake Waring, Lake Bonneville, and the Colorado River.

This greatly elongate enclosed fault basin extends almost due north-south. It resembles and parallels the Lake Steptoe basin, but starts and ends farther south. Its greatest length is 180 km. and its greatest width, north of the middle, is 42 km. A stretch as narrow as 21 km. lies south of the middle. The lake was 96 km. long and its maximum width was only 17 km. in the northern and 13 km. in the southern part. Between these two parts there appears to have been, at the highest lake level, a strait narrowing to about 3 km.

Lake Spring at its deepest filling was a large body of water, covering 978 sq. km., as we measure it. C. T. Snyder and associates, accepting a less elevated (and more certain) highest shoreline (see below) computed the lake area as 332 square miles = 860 sq. km. (Snyder *et al.*, 1964) or 335 square miles = 868 sq. km. (Snyder and Langbein, 1962, p. 2385). The corresponding estimates for the area of the drainage basin are 4,337 sq. km., 1,641 square miles = 4,253 sq. km., and 1,630 squale miles = 4,222 sq. km. According to these figures, the lake area comprised 23, 20, or 21 percent of the drainage basin. The close approximation of these proportions, despite a considerable discrepancy in estimates of the maximum depth (see below), is attributable to the steepness of the sides of the enclosing basin.

The great length and depth that Lake Spring attained is consistent with the towering height of the closely margining mountains. Except for passes, the ridge of the Snake Range to the east attains, for most of its length, altitudes higher than 2,500 m., exceeds 3,000 m. in several peaks, and reaches 13,063 feet (3,982 m.) at Wheeler Peak. Most of the Schell Creek Range, to the west, surpasses the altitude of 2,700 m.

The evidence that this entire valley has no native fish (see below) confirms the geomorphological indication that the basin is now and probably has long been wholly endorheic.

The hydrography of the basin has been treated and the pluvial lake mapped by Rush and Kazmi (1965).

Shorelines and Interior Drainage.

We have estimated the maximum depth of Lake Spring as approximately 95 m., on the basis of evidence cited below. This estimate is considerably higher than those presented by C. T. Snyder and associates. We have relied on indications of higher shorelines that are less bold and less completely certain than the ones on which they relied. Snyder *et al.* (1964) estimated the maximum depth as 265 feet (81 m.). Snyder and Langbein (1962, p. 2385) stated that "Spring Valley was filled to a depth of nearly 250 feet [76 m.] by its Pleistocene lake" and gave figures of 5,780 feet for the altitude of "the uppermost average stand of this lake, clearly marked by shoreline terraces" and of 5535 feet for "the

average altitude of the floor," a difference of 245 feet (75 m.).

We are of the opinion that the lake rose, probably intermittently, to considerably higher levels than 75 m., presumably without very long still-stands that would have produced strong shoreline features—but not to heights approaching the altitude of the gaps to the southward. The lake outline shown by Snyder *et al.* (1964) corresponds closely with the 5,800-foot (1,768-m.) contour on the Ely and Lund 1:250,000 maps. The Lund map depicts that contour forming a very tight loop about 3 km. long extending transversely across more than half of "Baking Powder Flat" in the southern expansion of the old lake floor, just short of the southern border of T. 13 N., R. 67 E. The dikelike structure, followed by Highline Road, we verified as a lake bar, which presumably was formed under water. Another bar is indicated by a tightly closed loop, 4.5 km. long, of the same contour, across the lake bed near its north end (shown on the Ely map in T. 20 N., R. 67 E.), and below this a complex of bars and dunes representing recessional levels of the lake. Gravel ridges trending north–south along the east shore near Worthington Spring, about opposite the major west-east bar of the southern basin, were estimated by altimeter readings, checked against the altitude of 5,878 feet near Shoshone entered on the Lund map, to be very close to the altitude of 5,845 feet (1,782 m.), 95 m. higher than the 5,535 feet (1,687 m.) given by Snyder and Langbein for the altitude of the old lake bed (the Ely map shows "5536" on White Lake, the present sump). Apparent high shoreline features on the east side of the valley, extending southward from near the base of the bajada just north of where U. S. Highway 6 and 50 turn southward, were judged when seen on July 5, 1959 to be at about the same altitude as the gravel ridges near Worthington Spring. The uppermost shoreline features are not boldly developed, nor would we expect them to be in the basin of a lake that did not discharge. Somewhat lower terraces are undeniable. Below the clearly marked feature at 5,780 feet Snyder and Langbein (1962) indicated six shoreline terraces.

By far the lowest passes around the rim of Spring Valley are three gentle divides near the south end of the basin, two into the basin of pluvial Lake Carpenter (pp. 65–66) and one into Snake Valley of the Lake Bonneville system. All three passes are close to the same altitude, which is well above any indicated level of Lake Spring. One of the two gentle passes between the Spring and Carpenter basins, the one followed by U. S. Highway 93 leading into the north end of Lake (Duck) Valley, is shown on the Lund 1:250,000 map as being not quite closed by the 6,200-foot (1,890-m.) contours. In the other pass between these two basins, leading toward the southern part of Lake Valley, the same contours barely cross over. The divide into Snake Valley is probably at almost the identical altitude, for although the same contours here cross the divide farther apart, the pass is extremely flat, as we observed in 1938. There are no obvious indications of a discharge into either Lake Valley or Spring Valley.

There are no indications that at any time, at least not during a late pluvial period, Lake Spring ever received any inflow of water from any adjacent basin or that it ever attained a discharge, either surface or subterranean. The passes are all too high for any surface exchange. As Snyder and Langbein (1962) indicated, the floor of Spring Valley is lower than that of any surrounding basin other than Snake Valley to the east, and the paucity of major springs argues against an underground outflow in that direction. The basin seems to be completely endorheic. Accepting this view, Snyder and Langbein concluded that their "studies of the hydrographic regimen that would be required to maintain a Pleistocene lake indicate that relatively small adjustments of evaporation and precipitation would be necessary. The most likely combination of adjustments among those possible suggests a 30 percent decrease in evapora-

tion rates and an 8-inch increase in precipitation." (See also p. 9.)

Remnant Waters.

White Lake, the shallow sump of the northern part of the Lake Spring basin, ordinarily holds some water, as it did in 1938, when Bert Robison and other informed residents told us that it had gone completely dry in the great drought of 1934, for the first time in many years. We were further told that in 1934 the valley became so dry that cattle had to be shipped out. Several of the trout creeks in the Schell Creek Range went dry. Even the largest one, Cleve Creek, failed in August to reach Cleveland Ranch in the valley. Only a few of the deepest of the many spring pools on the west side of the northern half of the valley retained water.

A considerable number of trout streams, incorrectly shown as wholly intermittent on the Ely and Lund 1:250,000 maps, flow to or toward the bed of Spring Valley from the Schell Creek and Snake ranges. Spring Valley Creek, coursing down the narrow northern arm of the valley, maintains a slight flow in the dry season and did not completely disappear in 1934. Other streams, on the arid alluvial slopes around both northern and southern ends of the valley, are intermittent.

In normal years, many spring pools, ponds, sloughs, marshes, and meadows exist on the west side of the northern half of the valley, and a spring is mapped on the west margin of Baking Powder Flat, to the south. The only extensive springs on the east valley edge are those on the Shoshone, originally Swallow, Ranch, near the base of the Snake Range south of Wheeler Peak. Here, in 1938, innumerable springs rose in an arc about 5 km. long. These and a few other springs feed many ditches and sloughs to form "The Seep" on Baking Powder Flat. Other ranches on the east side of the valley were said to rely almost entirely on mountain-stream water. Worthington Spring, near the north end of the southern expansion of the valley, on the east side, had already been piped in 1938.

Fish Life.

In our earlier report (Hubbs and Miller, 1948b, pp. 56–57) we mentioned taking in Spring Valley two native fishes, "a new sucker, with characters that line it up best with a Bonneville, or possibly a Colorado species," and the dace we have named *Relictus solitarius*. These we had taken only in a spring pool in the course of Spring Valley Creek, beside the Stone House (at the road junction west of center of T. 22 N., R. 66 E.), on the old Overland Mail Route, later the Lincoln Highway. We have since come to regard both species as having been introduced into the valley, probably at this old ranch. The evidence is presented in the species accounts for *Catostomus (Pantosteus) platyrhynchus* on p. 229 and for *Relictus solitarius* on p. 233. Another cyprinid, the Utah chub, *Gila atraria*, which we found to be well established in Shoshone Springs, we also regard as having been introduced, on the basis of testimony that it was brought in by Mormon settlers (p. 231). The cutthroat trout, *Salmo clarkii*, undescribed subspecies, that occurs in the mountain streams has also been indicated to have been introduced (p. 237, and Miller and Alcorn, 1946, pp. 177–178). Other species, unquestionably exotic, have been introduced.

PLUVIAL LAKES REGARDED AS HAVING BEEN TRIBUTARY TO COLORADO RIVER SYSTEM

We (Hubbs and Miller, 1948b, pp. 55, 96–100, 154, 164–165, figs. 25–29) have already regarded several basins, each with a pluvial lake, as disrupted parts of the pluvial White and Carpenter river divisions of the Colorado River system. Along with lakes Coal, Bristol, Delamar, and Carpenter, we should have included Lake Jake (pp. 57–58, 151, 159), but not the "lake in Long Valley" (p. 57), namely Lake Hubbs, which we now know to have been less disrupted from the basin of Lake Newark of the Lahontan complex (pp. 26–29). Among these various ancient waters, regardable as disconnected parts

of the Colorado River system, only two, Lake Carpenter and Lake Jake, are here treated in any detail.

Physiographic information now available on the Lund and Caliente 1:250,000 maps and on the 1965 United States Geological Survey 1: 500,000 map of Nevada, prompt us to enter a few remarks on some of the other basins. The basins of lakes Coal, Bristol, and Delamar, and the depression of Cave Valley, which Snyder *et al.* (1964) indicated to have contained a lake they named Cave, are now confirmed as being physiographically most closely related to the drainage of the pluvial White River system. However, the alluvial deposit in Pahranagat Valley that formed Maynard Lake (Hubbs and Miller, 1948b, p. 98, fig. 26) now appears less likely to have resulted from the ancient discharge of Lake Delamar, as we thought, than from an outflow from a canyon immediately south of Delamar Valley. The basin that contained Lake Delamar is essentially continuous with Dry Lake Valley, the site of pluvial Lake Bristol. There is a strong possibility, but as yet no definite evidence, that some or all of these lakes, all at most shallow, actually maintained a surface discharge into White River waters. The same holds true for the irregular chain of lake-containing valleys (p. 35) that extend between Railroad Valley and pluvial White River and may mark the course of a very remote discharge of Lake Railroad.

Pluvial Lake Carpenter

Drainage basin in extreme southern White Pine County and, chiefly, in Lincoln County, eastern Nevada (fig. 1).

We proposed (Hubbs and Miller, 1948b, pp. 98–100) for this ancient body of water the name Lake Carpenter, which has been accepted by Snyder *et al.* (1964) and by Feth (1964). Like most of the other depressed basins, it is represented at present by an extensive alluvial flat, that of Lake (or Duck) Valley.

The drainage basin of this ancient lake was bounded on the short northwestern sector by the Lake Steptoe basin and on a short northeastern sector by the Lake Spring basin; on the east side chiefly by the drainage of Lake Spring and very slightly by the Lake Bonneville watershed; around the south end by tributaries of what we have called pluvial Carpenter River (the presumed outlet of Lake Carpenter), a tributary to the pluvial White River and Colorado River systems; and on the west side by headwaters of pluvial White River and by affluents of Lake Cave, which probably discharged into White River.

The drainage basin and the lake were roughly similar in north-south orientation and in form. The basin was 72 km. long and, toward its south end, 34 km. in maximum width. Corresponding greatest dimensions of the pluvial lake were 38 and 11 km. The northern end of the basin and of the lake were pointed; the southern end, rounded.

We estimate that at its highest stage Lake Carpenter occupied 247 sq. km., or 20 percent of the area (1,257 sq. km.) of its drainage basin. The lake was obviously shallow, for the lowest altitude for the lake flat given on the Lund 1: 250,000 map is 5,915 feet (1,803 m.) and the outlet was somewhat below the 6,000-foot (1,829-m.) contour, indicating the lake depth as somewhat less than 26 m. This extensive accumulation of water is attributable to the circumstance that the elongate drainage basin was closely bounded by mountain ranges rising in general more than 600 m. above the lake level, and to the altitude of 3,254 m. at one peak, Mt. Grafton.

There was obviously no pluvial inflow of surface water into the basin of Lake Carpenter, although there were two low and gentle passes between this basin and that of Lake Spring (p. 63).

There is some disagreement as to whether Lake Carpenter rose high enough to discharge southward into the course of pluvial Carpenter River, an affluent of the Colorado through the lower

pluvial White River. Carpenter (1915, p. 44) indicated that the lake so discharged. He stated:

> During the humid Pleistocene epoch this lake drained southward into Meadow Valley through a channel about 50 feet deep and one-fourth mile wide. This channel begins at about the latitude of Poney Spring and becomes progressively deeper toward the south. East of Pioche Range it is about 100 feet deep in places and is cut through bedrock.

Snyder *et al.* (1964), however, claimed that the lake did not spill. Morrison (1965, fig. 1) indicated the outlet. If the lake did not overflow in late pluvial time, it may have done so on some early pluvial occasion(s). Although the passes to the Spring and Bonneville watersheds are also low, the one to the southward (to Carpenter River) seems to be the lowest. It is indicated on the Lund map as the lowest, just below the 6,000-foot (1,829-m.) contours, whereas the passes leading to the Lake Spring and Lake Bonneville watersheds are indicated, respectively, to be a little below and a little above the 6,200-foot (1,890-m.) contour. Present underground discharge through Patterson Wash was indicated by Rush and Eakin (1963).

Although we took no elevations, we are led from our reconnaissance of July, 1938, definitely to favor Carpenter's view that Lake Carpenter did discharge to the southward. Significantly, local testimony indicated that Wilson Creek, the main affluent to the lake bed (see below), in times of flood turns southward to join Patterson Wash, which definitely is in the southern drainage. Our field notes indicate, further, that there may be a low spot south of Geyser, but that even from there the general trend is southward (this point is not well verified by the few altitudes entered on the Lund map). From near Pony Springs (a little south of the pluvial lake as mapped by Snyder *et al.* and by us) there are beds and terraces of considerable magnitude, indicating a former river system (which would have been the head of pluvial Carpenter River).

REMNANT WATERS AND FISH LIFE.

The only extensive spring waters in the Lake Carpenter basin are those just south of Geyser Ranch, near the north end of the old lake bed. These waters discharge through very deep sloughs into a series of small lakes, in a broad area of wet marshes. On July 8, 1938, the water in a slough registered 20.0° C. (air, 21.1°) and contained considerable submerged and emergent vegetation. The only other springs near the lake bed are Pony Springs, on the west side near the south end. The only stream of any consequence in the basin is Wilson Creek, which flows northwestward toward the lake bed from the north side of Mount Wilson, the altitude of which is mapped as 9,296 feet (2,833 m.). On the next day, this stream, where examined 14.5 km. east of Pony Springs, was about 1 m. wide and 10 cm. deep, with a good current of clear water. The hydrography of the basin was treated by Rush and Eakin (1963).

On the same trip, we found no fish that surely appear native in any of the waters just mentioned. 'Trout' had been planted in Wilson Creek, which was posted as closed to fishing. No fish were seen in Pony Springs. In a spring-fed ditch in the complex of waters near Geyser we collected carp, *Cyprinus carpio*, and Utah chubs, *Gila atraria* (UMMZ 124790). Local residents were too new to know anything about the introduction of chubs, but the drainage relations are such as to render it virtually certain that they had been introduced. Some testimony indicates stocking from Utah (p. 231). Plausible sources nearby were the springs at Shoshone, where they were almost certainly introduced (p. 64), and Big Springs or the adjacent slough south of Garrison, Utah, nearby in the Bonneville Basin (a native habitat for the species).

PLUVIAL LAKE JAKE

Drainage basin in southwestern White Pine County, east-central Nevada (figs. 7, 13).

This, one of the smaller of the enclosed Pleistocene lakes, was named by us (1948b, pp. 57–58) Lake Jake, which designation has been accepted by Snyder *et al.* (1964) and Feth (1964).

The drainage basin is bounded by the watersheds of the following pluvial waters: Lake Hubbs to the northwest; Lake Gale very narrowly to the northeast; Lake Steptoe to the east; White River to the southeast and south; and lakes Railroad and Newark to the west.

The whole drainage basin is roughly diamond-shaped, 51 km. long by 32 km. wide, with a subcentral elliptical fault-block depression, Jakes Valley, roughly 34 × 17 km., lying between mountain fronts. Within the drainage basin, the depressed block and the lake are displaced to the eastward.

As mapped by Snyder *et al.* (1964), slightly larger than we did in our first report (Hubbs and Miller, 1948b, pp. 57–58), Lake Jake measured about 7 × 17 miles (11.3 × 27.4 km.) and covered a stated area of 67 square miles (174 sq. km.), 16 percent of the drainage basin of 429 square miles (1,112 sq. km.), and they indicated the depth of the non-discharging lake as 65 feet (20 m.). Although we have seen the basin only from near the north end of the ancient lake, we believe that these were underestimates of the size of the lake. We draw this conclusion from the cursory field observations, local testimony, and, particularly, from an examination of four 15-minute quadrangles (clockwise from northwest: Illipah, Riepetown, Preston Reservoir, and Treasure Hill).

We now compute higher values: the lake as measuring 12 × 31 km., covering an area of 249 sq. km. (22 percent of the drainage-basin area of 1,114 sq. km.), and the lake depth as 150 feet (46 m.). Thus, we compute the lake as slightly longer, 1.4 times greater in area, and 2.3 times deeper. We have arrived at our estimates as follows: The altitude of the central depression (without, however, a playa, according to local testimony) is slightly below 6,295 feet. This is the figure given in the Riepetown Quadrangle for Jake VABM (Verified Altitude Bench Mark), which is near the end of a dry wash. We approximate the lowest point as 6,292 feet (1,918 m.). On reasoning given below, we assume that the top level of probably occasional discharge is about 6,442 feet (1,964 m.), thus providing the estimate of 150 feet (46 m.) for the maximum depth of the lake.

A minimum approximation of the depth at least approaches 100 feet (30 m.), because the Riepetown Quadrangle shows, near the northwest corner of the lake bed, the interpolated contour of 6,380 feet (1,945 m.) in the form of complex bars that were presumably formed under water. These circumstances indicate a water depth in excess of 88 feet (6,380 – 6,292), or 27 m. In line with these data on a minimal size estimate we have mapped a second lake outline, as a dashed line at the 6,400-foot contour (1,951 m.), yielding estimates of 108 feet (33 m.) for the lake depth, of 26 × 11 km. for the major dimensions, and 186 sq. km. for the lake area (17 percent of the drainage-basin area). Other indications on the same and other quadrangles bespeak the reasonableness of these estimates. Nearby, in the axis of the bed of the lake, a labelled "Gravel Pit" suggests a beachline. On the east side, another "Gravel Pit" is shown, beside a verified-altitude benchmark at 6,363 feet (1,939 m.). Near the south end of the lake bed there is an ancient gravel bar (see below), which on the Preston Reservoir Quadrangle is designated by the suggestive term of "Railroad Crossing," just above the 6,360-foot (1,939-m.) contour, and this bar was presumably formed under water. Furthermore, apparently longshore features are mapped on the same contour on the Illipah Quadrangle (in Sec. 11, T. 16 N., R. 59 E.) and on the Preston Reservoir Quadrangle (near the southeastern margin of the old lake).

Several lines of circumstantial evidence lead us to regard as highly plausible the hypothesis that Lake Jake occasionally rose to, or at least well toward, the assumed outlet level, which lies near the north end of Jakes Wash. That long

flood-water course, in the headwaters of pluvial White River, is separated by a very low and gentle saddle from a wash, in the same linear depression, that runs northward onto the bed of Lake Jake. One line of evidence is that the basin is hemmed in by rather high mountains, the Egan Range to the east and the White Pine Range to the west. Tributaries forming a rather extensive system in the White Pine Mountains still carry water, feeding the sizable Illipah Creek (see below), and these mountains retain snow in winter.

The percentage of the area of the drainage basin that was covered by the lake (as now treated), namely 17 to 22 percent, is average for the whole area. This area is one where we would expect the fluctuations in precipitation to have been great. During unusually moist periods the lake might well have risen rapidly to or at least well toward the sill. The lack of a deep trench in Jakes Wash, however, is evidence that an outlet if attained was not greatly prolonged, or was so ancient that the channel has been obliterated by lateral aggradation.

Information regarding this basin, in part summarized by us (Hubbs and Miller, 1948b, p. 56), was obtained on June 26, 1942, from Mr. Moorman, the only rancher in the drainage basin (the Moorman Ranch is also mapped as Illipah, and the mountains margining the lake basin on the west form the Moorman Ridge). Jakes Valley, we have heard, was named for "Dutch Jake," the earliest settler at Illipah. Moorman's father came to Nevada in the 1860's and settled at Illipah in 1896. Mr. Moorman informed us that the valley has no dry lake bed, but to the south there is an oval white-sage area about 15 miles (24 km.) long, surrounded by lines of water levels, indicating successive recessions of the former lake. Across this, he said, is a broad bar of round stones somewhat cemented together, which we assume to be an ancient gravel bar, the "Railroad Crossing" (mentioned above). The bar had been broken in one place by a washout, which had been filled in to make a reservoir (shown on the Preston Reservoir Quadrangle) for stock.

Remnant Waters and Fish Life.

Mr. Moorman and ranch hands informed us that Illipah Creek is the only permanent stream in the basin, and reported its flow in the summer as 3–4 second-feet, all of which was used at the ranch. On June 26, 1942, at the mouth of the canyon about 1 km. above the ranch, the rather muddy, perhaps somewhat swollen stream, was about 3 m. wide and flowed over a stony bottom. Mr. Moorman said that the main creek (Halstead and Cottonwood creeks are tributaries) rises in a large permanent mountain spring. His further testimony was recounted by Miller and Alcorn (1946, pp. 177–178). Several other mountain springs are mapped at the headwaters of Illipah Creek, and on the south side of the northern divide.

According to Leigh (1964, p. 61), "**Illipah Spring** in Momoke Hill, near Little Antelope Summit, is a splendid spring gushing from a cleft in solid rock 2,000,000 gallons of water each day."

Mr. Moorman was positive that there are no native fish in Illipah Creek, or anywhere else in the basin. His testimony regarding the stocking of trout and other data on the introduction of trout into the creek was recounted by Miller and Alcorn. Mr. Moorman's statements we regarded as highly reliable. He well knew the minnows and suckers of White River to the south, where a rancher "used to fry the minnows in the round to eat." He noted also the use of such native fish for "coyote scent" and knew of minnows in various other waters where we had found them.

PLUVIAL LAKE PINE ("WAH WAH"), WITHIN BONNEVILLE SYSTEM

The vast hydrographic basin of Pleistocene Lake Bonneville, which, among the many divisions of the Great Basin, was approached in magnitude only by that of Lake Lahontan (in terms both of basin and lake), was essentially integrated, in strong contrast to the carved-up area we have under primary treatment. As the

great inland Bonneville sea desiccated, some basins, as those of Utah Lake and Sevier Lake, became independent. In addition, a few tributary lake basins of fault-block origin, charted by Jones (1940) and mentioned by us (Hubbs and Miller, 1948b, pp. 32, 148, 156), existed peripherally to Lake Bonneville at the top (Bonneville) level. One of them, though wholly surrounded by integrated parts of the Bonneville system, was relatively near the enclosed basins that we are now discussing, and has been included in the study.

It is possible that at some time more remote than we are emphasizing, some other basins may have been included in the Bonneville watershed, for the intervening passes are lower than those into other depressed basins. These are the Waring–Steptoe system and the basin of Lake Spring (see above).

The drainage basin of Lake Pine, that of Pine (= White Sage) Valley, lies in southwestern Millard County, in western Beaver County, and, very slightly, in northwestern Iron County, southwestern Utah (fig. 1).

Lake Pine was treated and named as a pluvial as well as a modern body of water by Jones (1940), as we noted in our brief treatment of the lake (Hubbs and Miller, 1948b, p. 32). The lake was renamed "Wah Wah" by Snyder *et al.* (1964). We prefer to retain the name Lake Pine on the basis of priority and because Wah Wah Valley, Wah Wah Springs, Wah Wah Field Station, and Wah Wah Dry Lake all lie to the eastward, beyond the Wah Wah Mountains.

Pluvial Lake Pine was unique among those herein treated in having been completely surrounded by the drainage basin of Lake Bonneville.

The drainage basin, as delineated from the Richfield 1:250,000 map and the Wah Wah Summit 15-minute Quadrangle, is 75 km. in greatest length (north–south) and 39 km. in maximum width, north of the middle. The basin is largely surrounded by the Needle and Wah Wah mountains, which converge southward, and an interpolated mountain at the north, between two rather gentle passes. The dimensions of the lake, as traced by us, were 15 km. long and, near the north end, 10 km. in maximum width.

Areal dimensions of lake and basin were given by Snyder *et al.* (1964) as 41 and 720 square miles, indicating that the lake covered 6 percent of the area of the drainage basin. Our essentially similar numbers are 102 and 1,912 sq. km. (5 percent).

This relatively limited accumulation of water may be attributed to the moderate height of the surrounding mountains, the rather low and broad passes to the north, the position in the rain shadow of the lofty Snake Range, and the southern location. Sharp southward decrease in surface-water accumulation in pluvial time, matching the present southward increase in aridity, has been indicated in the several general treatments of pluvial waters in the West. However, the basin still contains a live stream (see below).

The topographic maps now available, as well as the field reconnaissance, show clearly that the low passes between this wholly endorheic basin and the Snake Valley arm of Lake Bonneville were far above any possible lake levels, and the pass toward Escalante Desert was even higher. The doubts we expressed in 1948 (p. 32), when topographic data were not available, were unfounded. There are no suggestions of any inflow of surface water from any other basin.

These physiographic relations became evident to us in a reconnaissance of the basin on June 24, 1950. We found that there are definite indications of a beachline, and now note that these are approximately on the enclosed 5,200-foot (1,585-m.) contour on the topographic maps—the line that Snyder *et al.* (1964) apparently followed in charting the lake. Along the road from state highway 21 northerly toward the headquarters of the Desert Range Experimental Farm, a shoreline was suggested at 2.5 km. where the road is now mapped beside the 5,200-foot contour. At 4.0 km., at the gates to the Experimental Farm, still beside that contour, we encountered a sharp slope that seemed to surround the basin, at least

on the southwest side. At the Farm we obtained confirmatory evidence from Selar S. Hutchings and other staff members. They had also concluded that the top beachlines are approximately at the entrance gates. They had found tufa on rock along the lake terraces and showed us samples. These were taken at about the same level as the entrance gates, at places estimated to be about 2 miles from the playa and 100 feet higher (the depth of the lake was presumably nearer 200 feet = 60 m., for the top beachlines approximate 5,200 feet and an elevation of 5,086 feet is shown outside the playa). They mentioned further that clean gravel had been dug by the corral of the abandoned ranch near the 5,200-foot contour on the south side (such gravel is commonly of shoreline origin).

Remnant Waters and Fish Life.

The topographic maps show an ephemeral pond at the east end of the playa. The longest tributary, from the south, was found to be dry, but in T. 27 S., on the line of R. 16–17 W., the terrace-flanked valley, about 1 km. broad, indicated greater pluvial flow. At the time of our visit (June 24, 1950), an ample stream was flowing in the well wooded tributary Pine Grove Canyon, in T. 27 S., R. 16 W. (the place where pine lumber was said to have been obtained for the famous organ pipes of the Tabernacle in Salt Lake City). Where examined near its lower end in the mouth of the canyon, this stream was fishless, and we were told in 1950 by Otto Fife, a well informed naturalist at Beryl Junction, Utah, that the trout in Pine Grove Creek had been introduced.

FISH LIFE OF BASINS IN NORTH-CENTRAL GREAT BASIN

As indicated in our earlier summary (Hubbs and Miller, 1948b), correlating the hydrographic history and the residual fish faunas of arid western North America, four native fish species occur in the north-central part of the Great Basin herein under more detailed treatment. Their respective occurrences in the isolated and limited waters of the several basins are mentioned in the preceding discussions of these basins, and are outlined in tables 2 and 3.

GENERAL TREATMENT

Fish Fauna of Area: Its High Endemism and Extreme Depauperation

It is indeed noteworthy that only four native fish species have survived in the largely isolated springs in the north-central part of the Great Basin under special treatment, although the area involved embraces 54,028 sq. km. and is surrounded by the Lahontan, Columbia, and Colorado drainage basins, each of which is endowed with a much less depauperate fish fauna (Miller, 1958). These four indigenous species, however, include two relicts wholly endemic to the area, as well as representatives of two wide-ranging Western species, each much fragmented by local differentiation, which we interpret as being in part on the subspecies level. Such endemism is often characteristic of fishes that inhabit springs, even in areas where the fauna is much more profuse (as Armstrong and Williams (1971) have noted for the Tennessee River system).

One of the two endemic species, the relict dace (*Relictus solitarius*, pp. 196–226), representing also a genus of Cyprinidae confined to the area, occurs native only in two contiguous pairs of basins, each comprising a separate endorheic pluvial drainage system—that of lakes Franklin and Gale and that of lakes Waring (Lake Antelope excluded) and Steptoe (Upper Lake Steptoe excluded). This species occurs alone in these

TABLE 3. *Occurrences of native fishes in 21 pluvial-lake basins in the north-central Great Basin.*

Pluvial lake basins[1]	*Rhinichthys osculus*	*Gila bicolor*	*Relictus solitarius*	*Crenichthys nevadae*
Basins related to Lake Lahontan				
L. Gilbert	*R. o. reliquus*	—	—	—
L. Diamond	*R. o. robustus*[2]	*G. b. obesa*[3]	—	—
L. Diana	—	—	—	—
L. Yahoo	—	—	—	—
L. Newark	—	*G. b. newarkensis* *G. b. euchila*	—	—
L. Hubbs	—	—	—	—
L. Clover	*R. o. oligoporus* *R. o. lethoporus*	*G. b. isolata*	—	—
Basins related to L. Lahontan and Colorado R.				
L. Railroad	—	*G. b.* subspecies[4]	—	*C. nevadae*
Little Fish Lakes	—	*G. b.* subspecies	—	—
L. Lunar Crater	—	—	—	—
L. Snyder	—	—	—	—
Basins between Lahontan and Bonneville basins				
L. Franklin	—		*R. solitarius*	
L. Gale	—	—	*R. solitarius*	—
L. Waring	—	—	*R. solitarius*	—
L. Steptoe	—	—	*R. solitarius*	—
Upper Lake Steptoe	—	—	—	—
L. Antelope	—		—	—
Basin related to Bonneville and Colorado systems				
L. Spring			—	—
Basins tributary to Colorado River				
L. Carpenter	—	—		—
L. Jake	—	—	—	—
Basin surrounded by Bonneville system				
L. Pine	—	—	—	—

[1] Tributary relations shown by indentations.
[2] Slightly modified endemic races referred to *R. osculus robustus*.
[3] Strongly modified endemic races referred to *G. bicolor obesa*.
[4] Several subspecies, all undescribed.

two systems, which together comprise an area of 14,682 sq. km. (27 percent of the total study area). The many local populations of the relict dace in these systems, along with a few stocks in the basin of Lake Spring into which it was introduced, have been subjected to intensive analysis, to document the relict nature of the genus and species and its limited local variation. Together with the drainage basin of Lake Clover, the Franklin and Waring systems form the northeastern sector of the study area.

The other relict species, *Crenichthys nevadae* Hubbs (1932), represents a remnant genus (p. 227) of Cyprinodontidae with two fully distinct species, *C. nevadae* (p. 227), confined to Railroad Valley, the sump basin of the pluvial Lake Railroad (pp. 32–36) drainage basin, and *C. baileyi* (Gilbert), a relict endemic in the now isolated remnant waters of pluvial White River, which during the pluvial period(s) was tributary to the Colorado River (Hubbs and Miller, 1941, pp. 2–3). Both species are confined to hot springs in Nevada in the northernmost extension of the range of the Cyprinodontidae in western North America (Miller, 1958, pp. 205–207, fig. 15). The detailed systematic treatment of *Crenichthys* is deferred, but annotated synonymies of the genus and of *C. nevadae* are included (pp. 227–228).

along with a list of the known specimens of that species.

All other native fish of the study area are minnows that we refer to two species, *Rhinichthys osculus* and *Gila* (*Siphateles*) *bicolor*, each of which is widespread through western United States and is subject to almost endless local differentiation. All of the local populations within the area, of both species, have been subjected to extensive analysis, particularly to document the marked local differentiation, even within a single endorheic basin, that often has accompanied their isolation in the remnant spring waters. For both species the variational analysis has been extended to include populations from the Humboldt River system, taken to represent an approach to the presumed ancestral stock from which the deviating populations of the several basins arose. The basins that have retained remnants of *Rhinichthys* and *Gila* are those, along the northern edge of the pluvial-lake area of the Great Basin, that discharged in late pluvial time, or earlier, into Humboldt River of the Lake Lahontan drainage system. These basins, from west to east (fig. 1), are those of lakes Gilbert, Diamond, Newark, and Clover. The basins of lakes Diamond and Clover have retained both genera, that of Lake Gilbert retained only *Rhinichthys* (until its very recent apparent extinction), and that of Lake Newark has maintained only *Gila*.

That the *Rhinichthys osculus* and the *Gila bicolor* populations in the northern basins under treatment stemmed from the populations in the Humboldt headwaters seems obvious for a number of reasons. The physiographic evidence is strong and definite. Both species are ubiquitous in those headwaters, and almost certainly have been there through at least late Pleistocene time. Both species seem preadapted to survive in isolated waters. The characters of the isolated forms are plausibly derivable from those exhibited by the Humboldt headwater populations of *Rhinichthys osculus robustus* and *Gila bicolor obesa* (pp. 106–113, 151–153). Particularly significant is the circumstance that in various characters the Humboldt headwater races of *Gila bicolor obesa* very definitely approach the presumably derived forms occurring in the basins of pluvial lakes Diamond, Newark, and Clover, as is stressed in the systematic accounts (pp. 153–180).

The only other pluvial lake basin among the 21 herein treated that has retained two fish species is that of Lake Railroad, which contains, in addition to *Crenichthys nevadae*, as we have noted (Hubbs and Miller, 1948b, p. 91), a chain of differentiated populations of *Gila bicolor*, the detailed analysis of which is scheduled for subsequent publication. The *Gila bicolor* populations in the Lake Railroad basin (including the Little Fish Lakes subdivision) seemingly were derived from the basin of pluvial Lake Newark, by passage over the low divide (p. 35), as we have surmised (Hubbs and Miller, 1948b, p. 91). The only other *Gila bicolor* populations that have survived south and east of the Humboldt River system are those of Dixie Valley, the basin of pluvial Lake Dixie, and those of Big Smoky Valley, the basin of pluvial Lake Toiyabe. We believe (p. 14) that the Toiyabe population of *Gila bicolor* was similarly derived, along with *Rhinichthys osculus*, from the basin of pluvial Lake Gilbert. Cursory examination of the form of *Rhinichthys* in Big Smoky Valley leads us now to think that it warrants subspecific separation, though it definitely appears to have been derived from the Lahontan form, *R. o. robustus*. We have already indicated (Hubbs and Miller, 1948b, p. 44) that the *Gila bicolor* populations of the Lake Toiyabe basin appear to represent two endemic subspecies. These are yet to be described. The local representative of *R. o. robustus*, a subspecies in our opinion, has recently been described as a new species by Lugaski (1972).

To summarize, the four fishes that are indigenous to the 21 pluvial lake basins under discussion comprise two basic categories, which are strictly allopatric, except for limited sympatry in the large basin of pluvial Lake Railroad. These two categories, each made up of two species, are as follows:

(A) Fishes of widespread type that, in the north-central Great Basin, appear to have stemmed from past stream discharge into the major drainage basin of pluvial Lake Lahontan, through the Humboldt River system. These comprise two chains of local forms. The members of each group are treated as subspecies of a separate cyprinid species: *Rhinichthys osculus*, in the basins of pluvial lakes Gilbert, Diamond, and Clover, and *Gila bicolor*, in the basins of pluvial lakes Diamond, Newark, Clover, and Railroad (including the Little Fish Lakes subdivision).

(B) Two fishes of localized distribution, a cyprinid, *Relictus solitarius*, whose origin is not apparent, and a cyprinodont, *Crenichthys nevadae*, whose origin seems to date from some relatively very ancient discharge into the Colorado River system. The cyprinid is confined as native to the basin of pluvial lakes Franklin and Gale, and to the basin of lakes Waring and Steptoe. The cyprinodont is restricted to the central basin of the pluvial Lake Railroad drainage system.

The last two species listed, as noted before, appear to be old relicts, whose congeners are presumably to be found in the fossil record. Some information has appeared on the fossil history of *Empetrichthys*, the one near relative of *Crenichthys* (Uyeno and Miller, 1962), but nothing has been discovered regarding the paleontology of *Relictus*. In fact, no trace of Cenozoic fossil fishes has been unearthed in any of the 21 pluvial lake basins under treatment: a great pity. Such evidence should be diligently sought. A very impressive demonstration of light being thrown on the knowledge of the fish life in the Great Basin through paleoichthyological studies was accomplished by recent research on fossil fishes in the Lake Bonneville deposits (announced by Stokes, Smith, and Horn, 1964 and described by Smith, Stokes, and Horn, 1968). Recent expanding attention to the Cenozoic paleoichthyology of the West is very propitious.

Of the 21 pluvial-lake basins herein treated, 11 are now totally devoid of native fish life, 7 have retained one species (recently extinct in one basin), and only 3, as is mentioned above, have retained 2 species (table 3).

The faunal deficiency of the north-central Great Basin, throughout the drainage basins of the 21 pluvial lakes under current treatment, is exemplified not only by the great paucity of species retained in any of the endorheic depressions and the complete absence of native fishes in many of the 21 basins, but also by the lack of various taxa that would likely have persisted in the area if it had retained the profuse array of lakes and streams that existed in pluvial time. Such circumstances more than offset the retention within the area of two relicts: of *Relictus solitarius* in the Gale-Franklin and Steptoe-Waring drainage basins, and of *Crenichthys nevadae* in the Lake Railroad basin.

It is almost certain that native salmonoids are lacking, although subspecies of *Salmo clarkii* occur in surrounding basins. Their absence in the area being reported upon seems attributable to the very small size of the cooler mountain streams, from which native fish would presumably have been eliminated by the rare torrential floods. In addition, the streams of the Ruby and East Humboldt ranges, in the Franklin and Clover basins, were, it may be assumed, largely eliminated by the montane glaciation there (Sharp, 1938). Mountain whitefish of the genus *Prosopium* presumably occurred in the study area, for they have survived in the Bonneville and Lahontan systems to near their southern limits.

The families, genera, and species that failed to survive generally inhabit permanent waters of some magnitude, most commonly streams that persist onto the valleys, where they can resist lethal flushing by flash floods. In the basins under study they presumably succumbed to increasing aridity, because they were less preadapted than *Rhinichthys osculus* and *Gila bicolor* to the gross deterioration of surface waters that characterizes the north-central Great Basin.

The depauperation of the fish fauna of the north-central Great Basin is further emphasized

and particularized when attention is drawn to the considerable number of now extirpated families (Salmonidae, Coregonidae, Catostomidae, and Cottidae), of various genera and species, that almost surely abounded during some pluvial periods in at least some of the 21 basins under study. On the basis of their profuse retention in the adjoining Lahontan and Bonneville complexes (Synder, 1917; Hubbs and Miller, 1948b; Miller, 1962; La Rivers, 1962), and their survival in some of the adjoining basins, it is plausible to postulate that during pluvial times various other species occurred in two sets of drainage basins among the 21 treated.

It may be assumed that the basins that discharged into Lake Lahontan via Humboldt River (the basins of lakes Gilbert, Diamond, Newark, and Clover) harbored, in addition to the trout *Salmo clarkii* and the whitefish *Prosopium williamsoni* (Girard): suckers, *Catostomus (Catostomus) tahoensis* Gill and Jordan and *C. (Pantosteus) platyrhynchus*, and probably *Chasmistes cujus* Cope; another minnow, *Richardsonius egregius* (Girard), and a sculpin, *Cottus beldingi* Eigenmann and Eigenmann. Similarly, the basins that are thought to have discharged into Colorado River (the basins of lakes Carpenter and Jake and probably Railroad) presumably harbored Colorado River endemics, including suckers of the subgenera *Catostomus* and *Pantosteus* of the genus *Catostomus*, and the genus *Xyrauchen*; probably minnows of the tribe Plagopterini (Miller and Hubbs, 1960) and of the subgenus *Gila*; perhaps still other cyprinids; and perhaps also salmonoids (*Prosopium* and *Salmo*). Extirpation must have been the rule.

The concept of the extreme depauperation of the fish fauna in the many smaller, largely endorheic basins of the Great Basin is accentuated when attention is directed to the southern part of the Great Basin, where conditions both in pluvial and postpluvial time have been more arid than farther north. The entire area of the Great Basin south and southwest of the region under treatment, and south and southeast of the Lahontan system, excluding only the less depauperated Death Valley system (Miller, 1946, 1948) encompasses, as delineated and measured by Snyder *et al.* (1964):

- One pluvial lake basin, Toiyabe, of 3,354 sq. km., with two fish genera and species (*Rhinichthys osculus* and *Gila bicolor*, p. 72);
- Two pluvial lake basins, Dixie and Columbus, of 6,314 and 3,626 sq. km., respectively, each with a single species, *Gila bicolor* (and the Dixie basin includes the fishless Labou section, of 777 sq. km., and this species in the Columbus basin is confined to the Fish Lake tributary section, of 2,779 sq. km.);
- A total of 51 pluvial-lake basins, as recognized by Snyder *et al.*, comprising 42 drainage systems, occupying a total of 67,737 sq. km., all wholly devoid of any native fish life.

Of these 54 basins, the 3 that have retained fish obviously derived these from the Lahontan system, and some of the 51 now fishless basins presumably also had some connection with the Lahontan system.

Except for the Death Valley system (the pluvial Lake Manly complex), the drainage systems that have retained no fish into modern times constitutes 84 percent of the total vast area and 82 percent of the total number of drainage systems included.

The fish fauna of the Lake Manly complex has been treated by us (Miller, 1948; Hubbs and Miller, 1948b, pp. 77–88).

Reasons for the Depauperation of the Fauna, with Some Counteracting Differentiation.

Why only four fish species have survived in the basins of the 21 pluvial lakes under special consideration, and in only a few of the residual bits of water, and why these particular species have persisted, call for consideration. Plausible reasons are in part zoogeographical, dependent on paleohydrographic history, and in part ecological and physiological, dependent on adaptability to survival in dwindling waters.

Paleohydrographic circumstances include the

probability that in the north-central Great Basin ingression of any immigrants from the relatively rich Columbia River fauna has been blocked by reason of long-standing intervening contact between the tributaries of lakes Lahontan and Bonneville. There seems to be no evidence of any aqueous connection by which any members of the Bonneville fauna (richest in the Great Basin area) could have reached any of the basins under consideration, at least in late Pleistocene time. An ancient connection with the Colorado River system, probably early Pleistocene or earlier, presumably explains the occurrence in the Lake Railroad basin of *Crenichthys* (pp. 35–36), but no other fish representative of the Colorado fauna seems to have persisted in any of the endorheic basins under study.

The fishes of the desert basins under treatment have very seldom survived in any of the very limited waters other than springs, spring-fed pools, and short stretches of spring outflows, and are very largely restricted to waters of this type that rise near the margins of the playas, along the base of the adjoining mountains, ordinarily along more or less active faults. Such springs, though less inconstant than others, sometimes, as we have seen, stop flowing during extreme droughts (as in 1934), and many of them contain relatively few individuals, usually so crowded as to seem subject to destruction by predation or disease, even though all surface water does not disappear. In some basins only one or a very few springs have survived. Springs that rise on mountain slopes, and the springs and small streams that flow in the mountain canyons, often give the illusion of constituting possible to highly propitious fish habitats, and indeed for some time—even for years—may support introduced fish (trout, minnows, or suckers), but are devoid of native fish for a very good reason: the occasional torrential precipitation characteristic of such desert regions, striking locally only at intervals of years, decades, or even centuries, transforms the trickling waters into raging torrents that roll boulders, sometimes as large as a house, and flush everything onto the normally dry playas. There, the waters usually recede and disappear too rapidly to permit the fish to wend their way backward to habitable waters. At times water may persist for months or even years on the playas, but becomes too alkaline and too ephemeral to support fish. Trout that succeed well under ordinary conditions are occasionally, as is well known, wiped out, so as to require restocking. We have encountered several instances in which minnows or trout have thus been eliminated from waters wherein they had persisted for a few to many years, even from pluvial time.

The environment indeed has been so harsh that it is a wonder that any populations have survived. However, all four of the species that occur in the basins we are treating have exhibited exceptional ability to survive under the harsh conditions imposed by the very limited and isolated aquatic habitats of the arid American West. *Rhinichthys osculus* and *Gila bicolor* display such adaptation (perhaps in part preadaptation) over a wide area, and are the only fish species that have held out in any of the Great Basin waters under treatment, other than the two endorheic systems inhabited solely by *Relictus solitarius* and the one endorheic basin inhabited, along with subspecies of *Gila bicolor*, by *Crenichthys nevadae*. Both *Relictus* and *Crenichthys* have also dramatically demonstrated their ability to persist in isolated spring waters. In occasional streamlets, especially those that maintain flow onto the valley floor, minnows have become, or have remained, adjusted to the tenuous conditions (for example, *Rhinichthys osculus* in Indian Creek in Crescent Valley—p. 106).

One circumstance that to a degree has counteracted the depauperation of the fish fauna of the north-central Great Basin has been the trend toward raciation and even subspeciation, in correlation with the sharp isolation of the remnant stocks since pluvial time, not only between the populations in different endorheic basins, but also within some of these relatively small basins. Thus, we have found differences that we interpret as

being on the subspecies level between the populations of *Rhinichthys osculus* that have survived in the basins of pluvial lakes Gilbert, Diamond, and Clover, and between the stocks of *Gila bicolor* that have persisted in the basins of lakes Diamond, Newark, Clover, and Railroad. Within single basins we have recognized as on the subspecies level different populations of *Rhinichthys osculus* within the Lake Clover basin and of *Gila bicolor* within the Lake Newark and Lake Railroad basins. The two populations of Diamond Valley referred to as variants of *Gila bicolor obesa* approach the subspecific level of separation as a unit and are well differentiated from one another racially. Slight racial distinction seems evident between the two stocks of *Rhinichthys osculus oligoporus* in the Clover Valley section of the Clover basin, and between the several populations of *R. o. robustus* occupying separated springs in the basin of Lake Diamond. No strong differentiation, however, was noted between the now generally isolated populations of *Relictus solitarius*, even between those inhabiting the two separated basin complexes (Franklin-Gale and Waring-Steptoe). Gene interflow between the ordinarily separated populations of this genus, and of the other genera, following interconnection during the rare occasions of local torrential precipitation, may well have dampened the rate of regional differentiation.

Limited Sympatry

The extremely limited incidence of species sympatry in the arid region under treatment even more strikingly emphasizes the harshness of fish environments, the heavy toll by extinctions that must have occurred, and the resultant depauperation of the fish fauna. Even within the three basins among 21 that contain more than a single species, the two that they harbor are sympatric largely in the sense of occupying the same drainage basin. In the entire area covered, of 54,028 sq. km., encompassing a large part of one of the largest states in the country, two native species have been found, during extensive reconnaissance, to occur together in only three isolated springs! The limited degree of precise sympatry becomes increasingly evident when the circumstances are considered for each of the three basins that contain two species.

In the immense drainage basin of pluvial Lake Diamond (8,097 sq. km., including the Lake Diana and Lake Yahoo drainage basins), *Rhinichthys osculus* occurs alone in the following widely separated locations: R5, Potts Ranch; R5A, Dianas Punch Bowl; R6, Coils Creek; and R8, Big Shipley Spring (fig. 3). *Gila bicolor* occurs alone at only one location (G6), Sulphur Spring. At only one place, Birch Ranch (R7, G5), were the 2 taken together, and it is doubtful that they occur together elsewhere in the drainage basin, but here, so far as we could see, the species freely associate.

In the basin of pluvial Lake Clover (fig. 12), of 2,624 sq. km., *Rhinichthys osculus* lives alone at two locations (R10 and R11), both in Clover Valley, and occurs with *Gila bicolor* in the only habitable spring complex, Warm Springs, in Independence Valley (R12, G11, the one spot where *Gila* lives in the drainage basin). Even in this small spring area the two species are not completely sympatric in the strictest sense, for *Rhinichthys* is the more secretive and holds out in the denser vegetation, whereas *Gila* swims more freely in the limited available open water. They, therefore, though definitely sympatric in the geographical sense, are not completely associated ecologically (they are syntopic, to use a term advocated by Rivas, 1964).

Throughout the vast drainage basin of pluvial Lake Railroad, comprising 10,874 sq. km. (including the drainage basin of Little Fish Lakes), *Gila bicolor* inhabits many springs, including the sump basin of Lake Railroad, to which *Crenichthys nevadae* is strictly confined. But here the two species are almost completely segregated from one another: *Gila* monopolizes the cool springs and *Crenichthys* takes over in the hot springs. At only one place, not in a spring proper, were both

collected: in Duckwater Creek about three miles above Duckwater Store 445 specimens of *Gila bicolor* were taken on September 9, 1934, along with 23 strays of *Crenichthys nevadae*. Furthermore, recent field work indicates that neither species now inhabits this creek.

In all other drainage basins in the vast study area that have retained native fish only one species has persisted (tables 2, 3): *Rhinichthys osculus* alone in the single fish habitat in the drainage basin of pluvial Lake Gilbert (and it was apparently exterminated between 1938 and 1959); *Gila bicolor* alone in the few fish-inhabited springs of the Lake Newark drainage basin and in all of the habitats of the species in the several divisions of the Lake Railroad drainage complex other than the one mentioned above; and the relict dace, *Relictus solitarius*, alone in the many fish-harboring springs of the Franklin-Gale and Waring-Steptoe drainage basins. The possibility that *Gila bicolor* occurred in Ruby Lake of the Lake Franklin basin prior to the establishment of bass, *Micropterus salmoides*, is, however, not completely excluded, though we think the joint occurrence to be highly improbable (p. 209).

It would be difficult indeed to find any other fish-inhabited section of the world, of comparable size, which has been so devoid of competition between fish species!

Areas of Basins Correlated With Richness and Diversity of Fish Faunas

In our earlier report (Hubbs and Miller, 1948b) we pointed out that, in a general way, for the Great Basin province, a positive correlation exists between the area of a drainage basin and the richness of its fauna. This conclusion is consonant with a commonly held hypothesis for areas and species in general, particularly in connection with islands (MacArthur and Wilson, 1967, chapter 2). As is generally recognized, isolated drainage basins are, in effect, zoogeographic islands. The data (tables 2–4; fig. 15) for the basins under present study, and for a major selection of other parts of the Great Basin, comprising in all 426,316 sq. km. (as measured respectively by us and by Snyder *et al.*, 1964) fall in line with the general hypothesis, and seem reasonable on the assumptions that there have been many extinctions and that chances for survival have been greater in the more numerous and more diverse habitats provided by the larger areas. The coefficient of correlation between area and number of species, for the total drainage basin of the pluvial lakes entered in table 4, is 0.56 ± 0.10. Obviously, the diversity of the fauna, as indicated by the number of genera and of families represented (also shown in table 4), is also positively correlated with the area of the drainage basin.

The major irregularities in correlation between the area of drainage basins and the number and diversity of species, as shown in table 4, are largely explainable. The anomalously high number and diversity of species for the Bonneville (no. 1), Malheur (6), Goose (29), Truckee (34), Tahoe (48), Eagle (54), Long Valley (56), Ash Meadows (64), and Horse (67) drainage basins are attributable to the long or complete connection of the waters in these basins with a larger water system below, having a relatively large and diverse fish fauna. The entries for these basins are all those shown on figure 15 to the left of and above the dashed line. Most of the larger basins with no fish species, or with only one or two, are particularly arid.

The validity of the indicated positive correlation between the areas and the number and diversity of species is not thrown into question by the particular selection of basins that was made for the purpose of tabulation and computation. We have included all pluvial basins that contained a Pleistocene lake, as recognized by Snyder *et al.* (1964), for the north-central part of the Great Basin under special study, for the Lahontan system, and for the area farther northwest, and for the Death Valley system (Miller, 1946, 1948); also for Lake Bonneville. We do not include "Hot Creek Lake" and the "lake in Egan Valley,"

TABLE 4. *Correlation of areas of selected Great Basin pluvial-lake drainage basins with richness and diversity of native fish fauna.*

Including all basins that contained a Pleistocene lake, as listed by Snyder *et al.*, with exceptions discussed in the text (p. 77). Lakes with names marked by an asterisk are those dealt with in the present report. Data graphed in figure 15.

Pluvial drainage basin		
Name of lake	Area sq. km.[1]	Fish fauna[2]
1. Bonneville	138,112	4-9-21
2. Lahontan	109,614	4-9-11
3. Manly	53,224[3]	3-5-11
4. Panamint	20,629	3-4-4
5. Searles	16,408	3-4-4
6. Malheur	14,134	4-8-9
7. Owens	10,969	3-4-4
8. *Railroad	10,874	2-2-2
9. Tecopa	10,567	2-3-5
10. Mohave	10,502	1-1-1
11. *Waring	9,411	1-1-1
12. Manix	9,363	1-1-1
13. *Diamond	8,097	1-2-2
14. Catlow (incl. Guano)	7,656	1-1-1
15. Warner	6,858	2-4-4
16. Dixie	6,314	1-1-1
17. Alvord	6,066	2-2-2
18. *Steptoe	5,462	1-1-1
19. *Franklin	5,271	1-1-1
20. Fort Rock	5,219	2-3-3
21. *Spring	4,337	0-0-0
22. Crescent	4,237	1-1-1
23. Chewaucan	3,859	2-3-3
24. Surprise	3,836	2-2-2
25. *Newark	3,587	1-1-1
26. Toiyabe	3,354	1-2-2
27. Bristol	2,979	0-0-0
28. Adobe	2,901	0-0-0
29. Goose	2,875	5-7-7
30. Fish (White Mts.)	2,779	1-1-1
31. *Clover	2,624	1-2-2
32. Pahrump	2,569	1-1-1
33. Coal	2,541	0-0-0
34. Truckee	2,479	4-7-8
35. Granite Springs	2,476	0-0-0
36. Wellington	2,383	0-0-0
37. Madeline	2,163	1-1-1
38. Mono (Russell)	2,056	0-0-0
39. Alkali	2,038	1-1-1
40. *Gale	1,933	1-1-1
41. Meinzer	1,922	1-1-1
42. *Pine (Wah Wah)	1,912	0-0-0
43. Harper	1,865	0-0-0
44. High Rock	1,813	1-1-1
45. *Hubbs	1,677	0-0-0
46. Indian Springs	1,660	0-0-0
47. *Gilbert	1,528	1-1-1
48. Tahoe	1,427	4-7-9
49. *Diana	1,339	0-0-0
50. *Lunar Crater	1,321	0-0-0
51. Buffalo	1,318	0-0-0
52. *Carpenter	1,257	0-0-0
53. *Little Fish Lakes	1,131	1-1-1
54. Eagle	1,127	3-5-5
55. *Jake	1,114	0-0-0
56. Long Valley	997	2-3-3
57. Delamar	997	0-0-0
58. Carico	966	1-1-1
59. Cave	922	0-0-0
60. Kumiva	917	0-0-0
61. *Antelope	870	0-0-0
62. *Upper Lake Steptoe	816	0-0-0
63. Labou	777	0-0-0
64. Ash Meadows	756	2-3-4
65. Washoe	251	1-1-1
66. Lemmon	241	0-0-0
67. Horse	210	2-2-2
68. Spanish Spring	186	0-0-0
69. *Snyder	148	0-0-0
70. Laughton	129	0-0-0
71. Summit	98	0-0-0
72. Fred	57	0-0-0
73. *Yahoo	44	0-0-0

[1] Entire area tributary to lake named, including areas (also tallied) of basins of lake within the total watershed.
[2] Families—genera—species.
[3] Including Panamint, Searles, and Owens (excluded by Snyder *et al.*)

which we do not accept, at least as late Pleistocene, nor Lake Reveille, which we interpret as having been part of Lake Railroad at maximum level. The drainage basins that we have omitted, among the total pluvial-lake basins as listed for the Great Basin by Snyder *et al.* (1964), are all wholly fishless, and they are all in the southern part of the Great Basin, south of the Lahontan system and the basins particularly included in the present study, in an area that is now extremely arid and was presumably moderately arid even during the height of the pluvial periods, as we have stressed (Hubbs and Miller, 1948b). Many were probably shallow or even intermittent or dubious, and not one appears to have left a bold shoreline. The 38 fishless drainage basins involved, as listed, contained 45 pluvial lakes, of which Lake Columbus is thought to have re-

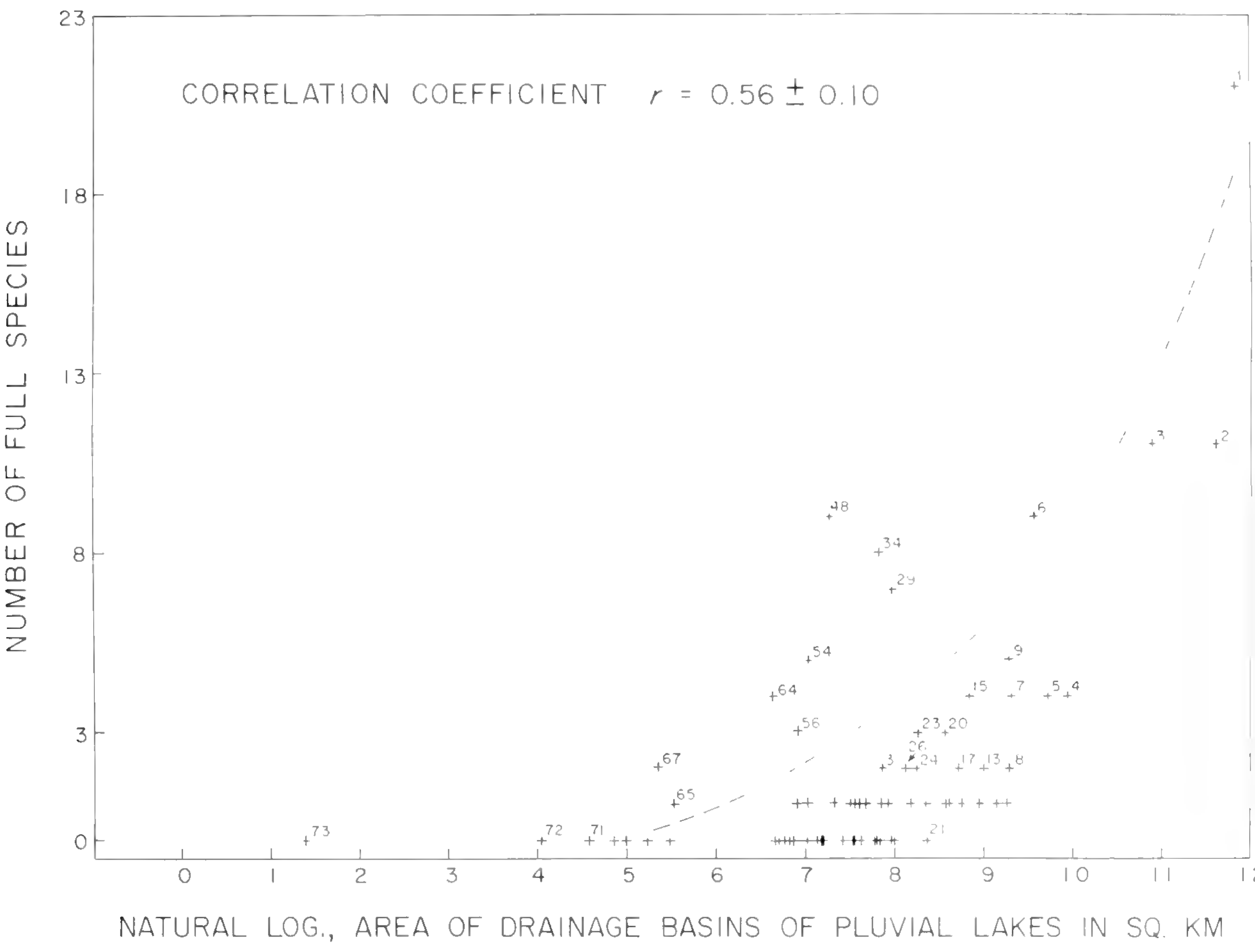


FIGURE 15. Correlation between area of selected pluvial-lake basins in Great Basin and number of native fish species. Data and lake numbers from table 4.

ceived the outflow of Lake White Mountains (Fish), which has a single native fish species, and is included in table 4. The listed areas of these 38 basins range from 78 to 8,094 sq. km.; only 11 exceed 2,000 sq. km.

Scrutiny of the data for the preceding discussion of the relation between the area of basins and the richness and diversity of the fish faunas throughout the Great Basin indicates that the north-central part, which we are particularly treating, is representative of the whole area, except for the three largest and faunally richest basins, those of lakes Bonneville, Lahontan, and Manly. The key feature is the trend toward fish-faunal extinction in the smaller, more isolated, and more arid drainage basins.

CHARACTERS AND SYSTEMATIC STATUS OF SPECIES

Our systematic analyses of *Rhinichthys osculus*, *Gila bicolor*, and *Relictus solitarius*, of the subspecies and local races of the first two, and of the local populations of the relict dace, have been based, primarily but not exclusively, on various measurable and countable features. Various items of size, general form, coloration, development of sensory structures (pores and barbels), dentition,

dimorphism in secondary sexual characters, numbers and size of individuals, and biomass are accorded attention. Other emergent methods of evaluating relationships, such as biochemical tests, karyotype analyses, behavior studies, and genetic experiments, would no doubt add much to the security of conclusions and to a fuller understanding of the origin and differentiation of the various isolated populations. Except for a start on karyotyping (p. 193), these promising approaches almost wholly remain to be undertaken. Transference experiments and the analysis of characters of fishes incidentally established into different types of habitat may often be a propitious means, and the most feasible way, to infer the genetic fixity of characters or the direct effects of altered environments (indeed one such test—in effect a natural experiment—was made by us on a population of *Rhinichthys osculus* that had been transferred, as bait minnows?, from one of the headwaters of Humboldt River into an isolated spring in Ruby Valley—p. 107). It is our hope that our studies will encourage others to expand the knowledge of the remnant fish life of the arid American West.

The characters of the fishes in the north-central Great Basin very largely reflect their adaptations to the spring habitats to which they are mainly restricted. These features, which they tend to share in common, are treated below, under the heading of Color, Texture, Form, and Sensory Structures.

The sharply restricted and concentrated ranges of the forms under treatment, along with their abundant populations, have made it possible to obtain comprehensive material for an analysis of the patterns of variation in various characters, and to learn something of population structure. It is indeed seldom that samples can be obtained so representative of whole populations throughout their range. We have tried to take some advantage of this potential, but further studies are surely in order.

We now proceed to a discussion of the several sets of characters that we have analyzed, treating definitions, methods, and procedures, as well as offering some evaluation of the characters. The actual presentation of the basic data, and their application to specific problems, are deferred to the accounts of each form or population. The order of presentation in the following discussion mainly follows the sequence adopted in the descriptions of the various local forms.

Size.

For all collections studied, we present the range in standard length for all specimens and indicate whether the fish are dwarfed, as are many isolated forms of restricted waters. It develops that the members of some of the isolated populations of greatly restricted range herein treated instead of being markedly dwarfed are larger than usual. For example, in *Rhinichthys osculus*, although *R. o. lethoporus* of Warm Springs in Independence Valley and the population of atypical *R. o. robustus* of the warm springs of Potts Ranch and the nearby Dianas Punch Bowl in Monitor Valley are greatly dwarfed, *R. o. reliquus* of the Grass Valley spring, the Coils Creek population of *R. o. robustus*, and especially the Indian Creek stock of that subspecies, are unusually large for the species. *Gila bicolor isolata* of Warm Springs in Independence Valley is somewhat dwarfed, whereas *G. b. euchila* of Fish Creek Springs in Newark Valley is unusually large and massive for an isolated population. The different populations of *Relictus solitarius* also vary widely in the size attained: the largest specimen among each of 21 collections containing 147 to 1,073 individuals had attained the standard length of 81 to 99 mm., but one other lot (Collection 17) included many large specimens, up to 114 mm.; 7 lots, in contrast, represent apparently dwarfed stocks, with greatest standard lengths of 41 to 77 mm. Very large specimens, incidentally, tend to have carried growth changes in proportions to an extreme (p. 214, fig. 51). As a whole, however, the native fishes of the isolated waters, many of greatly reduced area, are small.

Color, Texture, Form, and Sensory Structures.

The remnant fishes of the north-central Great Basin, as of other parts of the arid West, exhibit marked convergence in this complex of characters by reason of their long restriction largely to small isolated bodies of water with little current and with little or no competition and predation. They tend to be relatively sluggish, seeking shelter close at hand, rather than by dashing far away (as is noted below). They are in general midwater swimmers in quiet water. Seemingly molded by adaptation to their physical and biological environment, they tend to share various characters, which have mostly been pointed out already (Hubbs, 1940, p. 201; 1941a, p. 68; 1941b, p. 187; Hubbs and Miller, 1948b, pp. 51–52). These features are notably exhibited by the highly restricted spring dace *Eremichthys acros* (Hubbs and Miller, 1948a, pp. 20–27, pl. 1).

These spring fishes tend to be small, or even dwarfed; to be plainly and dully colored; and they, especially the females, tend to be relatively soft in flesh and texture. In correlation with life at mid-levels in quiet water, they tend to be chubby in general form, with the contours of head and body well rounded; and the ventral contour ordinarily approaches the dorsal contour in curvature, rather than being flattened as it is in related fishes adapted to current. The spring fishes are rather poorly streamlined, with a relatively deep caudal peduncle (not slender and with expanded procurrent caudal rays as in swift-water forms). Their mouths are usually more or less enlarged, terminal, and oblique, and are thus fitted for midwater feeding (not small, inferior, and horizontal, as in bottom-feeding rheophiles). Their fins, seemingly ample for limited locomotion in quiet, restricted waters, tend to be small, short, rounded, and supported by rays reduced in number and strength (rather than being elevated or prolonged, falcate, and with rays strong and not reduced in number, as in rheophiles). Their anterior parts are generally enlarged, at the expense of the often considerably shrunken posterior parts; as a consequence the dorsal and anal fins are commonly set far back. The scales of the spring types tend to be loosely arranged, poorly imbricated, deeply embedded, and often with the radii on all fields. Particularly notable is the tendency toward reduction or even obsolescence of the sensory canals and pores, the barbels, and other dermal sense organs, on both body and head; seemingly such structures are not very critically needed in the reduction or absence of predation.

The extent to which these trends have been carried in the spring-inhabiting fishes of the Great Basin is outlined in the descriptive accounts of the various forms. Such degeneration is particularly well illustrated by the isolated forms of *Rhinichthys osculus* and is moderately evident in *Relictus* (p. 181). Tendencies in that direction are shown by the isolated races of *Gila bicolor*.

Development of barbels. The degeneration of the barbel is particularly striking in the isolated forms of *Rhinichthys osculus*, the only species under treatment that ever develops this sensory structure. The degree of development of the barbel is discussed under the heading for that minnow (pp. 100, 104), and, in quantified detail, in the accounts of the respective subspecies.

Development of lateral-line pores. The tendency for the lateral-line pores to degenerate in the isolated spring populations involves both those along the lateral line of the body and those on the head canals. Some complexities arise in quantifying the degree of development. The measure chosen is the number of pores, which need to be separately tallied by size groups of fish, because the pores are not formed in the very young and develop rather slowly, increasing even into half-grown stages (see figs. 25 and 26 and table 12 for *Rhinichthys*).

The first pore counted ordinarily lies well behind the pore at the junction of the supratemporal head canal with the main lateral line. The arrangement, however, is subject to potentially confusing variation. When, not infrequently, no pore opens at the junction, the pore following, usually very closely, is disregarded in the count. The

pore that is usually counted first forms very early, so that many young specimens yield a count of 1. Near the beginning of the lateral line on the body numerous aberrancies in the canal and pores occasionally occur, such abnormalities as breaks and branches and the development of two pores on a scale. Especially in forms with a reduced lateral line, there are many irregularities along the whole line, with very frequent interruptions. Development of pores usually progresses from fore to aft, but as the formation proceeds, a secondary center often appears posteriorly, and almost always this occurs well before the caudal base. In larger specimens, however, pores sometimes form on the terminal scales, including occasionally one or two scales over the caudal-fin base (such pores have been included in the count). Interruptions, often extremely numerous, cause complications, for isolated single scales often form a tube with a pore at either end. Pores often form on either side of a break that is later closed in, so that only one is now counted where two would have been enumerated earlier. For such reasons, degenerative tendencies may lead to increased counts. In this study we have held to the criterion of counting each separate pore, even though the roofing-over of the canal is not complete. Often pores can not be detected where scales have been removed; for this reason, some counts are doubtless somewhat too low. However, care was taken to count specimens with few lost scales, and such omissions as have occurred have presumably not seriously vitiated the presentations or conclusions.

The lateral-line canals and pores of the head of the cyprinid species were extensively examined, and were found in general to follow the usual pattern for American genera as outlined by Illick (1956). For all forms treated, the degree of interruption of the supratemporal canal seems to be an important feature, and was tallied, with some counts; ordinarily the interruption occurs on the midline, and can be determined under due magnification with the use of a jet of compressed air. For *Relictus solitarius*, counts are presented of the preoperculomandibular pores.

These sensory characteristics are more closely correlated with the environment than with relationship, as is noted above.

In correlation with their reduced sensory equipment, the spring-inhabiting remnants exhibit less escape reaction than stream-inhabiting relatives. Thus, the creek race of *Rhinichthys osculus* in Crescent Valley showed much more escape behavior than the spring form in Grass Valley (p. 106). A special adaptation of spring forms seems to be their propensity to remain in the safety of the spring heads, avoiding impermanent outlet ditches, as noted for *Gila bicolor* in Sulphur Spring, Location G5.

Scale Structure.

Scale structure (fig. 46) was examined and is briefly described for the forms of *Rhinichthys osculus* and *Gila bicolor*, and for *Relictus solitarius*, with particular reference to the occurrence or lack of radii on the lateral and posterior fields as well as the anterior field; to the sharpness of the distinction between the fields; and to the general shape, whether essentially oval, or shield-shaped with strong angulation of the circuli along the line between the posterior and lateral fields. In this last respect considerable variation was found in *Gila bicolor*, but a preliminary suggestion of regional differentiation was not confirmed by further examination.

Morphometry.

In measuring the various body and head parts to check on local variation in the proportions we have adhered to the following methods (essentially as proposed by Hubbs and Lagler, 1964, pp. 24–26). Precision dial calipers were used and read to 0.1 mm. and all measuring was from point to point, by one of us (C.L.H.), usually on consecutive days, to help insure uniformity. Appropriate magnification and illumination were employed.

Our numerous samples of the Great Basin native fishes proved favorable for proportional mea-

surements, because they were uniformly hardened in 10 percent buffered formalin, then transferred in due time, after thorough washing, into ethyl alcohol. In general, the fish preserved well, with little twisting or opisthotonus. Furthermore, the skin remained firm and leathery, and the fins were tough, so that the specimens were little damaged (except for fraying of the caudal in some specimens), even when they had been carried (regularly in full glass jars) on the rough roads of 1934 and 1938. For most collections, the large series helped to prevent damage in transit and rendered it feasible to select for measuring very well preserved specimens of both sexes, of graded size.

As a reasonable check on differences in body, head, and fin parts the following measurements were taken:

1. Standard length in mm. (consistently used, even when not so stated).
2. Predorsal length (one tip of calipers was inserted at base of first rudimentary ray).
3. Anal to caudal (from extreme front of base of first anal ray to end of hypural on midline).
4. Pelvic to anal (from insertion of pelvic fin to origin of anal fin, as in item 3). Taken only for *Gila bicolor*, which shows some difference between populations in this dimension.
5. Body depth (greatest).
6. Peduncle depth (least depth of caudal peduncle, disregarding a slight constriction, when it occurred near origin of procurrent rays).
7. Head length (including opercular membrane).
8. Head depth (occiput to isthmus, even if slightly oblique).
9. Head width (greatest).
10. Snout length.
11. Orbit length (may be oblique; between true fleshy rims of orbit, disregarding puffy conjunctival tissue).
12. Upper-jaw length (to end of maxillary under suborbital).
13. Mandible length (omitted for *Rhinichthys*, in which the mandible is small and the mandibular joint is difficult to perceive).
14. Interorbital width (least).
15. Suborbital width (very definitive, by taking care to avoid puffy conjunctival tissue).
16. Depressed dorsal (from structural base at front, where one point of calipers was appressed rather firmly, to extreme tip of whatever dorsal ray extended farthest). The anal fin was not measured, as its length seems to be correlated very closely with that of the dorsal fin.
17. Caudal-fin length (from base of middle rays to extreme tip of longest ray, in either lobe; since caudal rays are particularly subject to breakage, fewer measurements are often given. Care was taken to limit this measurement to specimens with at least very nearly complete ray tips).
18. Pectoral-fin length (extreme).
19. Pelvic-fin length (extreme). In measuring the paired fins (from upper/outer base), care was taken to avoid the often commonly broken tips, and often the larger of the paired fins was measured.

In addition, the longest gill-raker was measured, in *Gila bicolor* only, as discussed below (p. 146).

The measurements, transformed into permillages of the standard length, are presented separately by subspecies or populations for large-size groupings of each sex. Further analysis of *Rhinichthys osculus* and *Gila bicolor* is presented for only a few, more critical dimensions. More detailed morphometry was carried out for populations of *Relictus solitarius*. The large mass of primary measurements have been retained and can be made available should occasion arise for further analysis.

The limited analysis so far attempted shows not only some useful differences between populations, but also demonstrates changes with age and the rather sharp sexual dimorphism that develops in all three cyprinid genera in the area.

Sexual Dimorphism and Nuptial Characters.

In all three species under detailed treatment, as in most cyprinids, males contrast with females in their smaller size, appreciably firmer flesh, and less posteriorly inserted dorsal fin. In other respects, the fins exhibit conspicuous sexual dimorphism, becoming in the males not only relatively longer but also stronger, with thicker rays. The pectorals and the pelvics become strongly modified in the nuptial males, with the anterior (or outer) rays and surrounding tissues especially enlarged; and these fins become more expanded. The pectoral in particular becomes greatly dilated transversely, stands out, and is somewhat twisted. The distinction is developed early, and increases with age and size, except that some very large females were noted to slightly approach the condition of males.

The nuptial tubercles, especially on the pectoral fin, are sharply distinctive in the three genera. Those on the head are outstandingly diagnostic in *Relictus*.

Sexual dimorphism and nuptial tubercles are treated under the headings of *Rhinichthys osculus* (p. 98) and subspecies (pp. 113, 121, 125, 133); subspecies of *Gila bicolor* (pp. 152, 156, 161, 166, 172, 179); the genus *Relictus* (p. 182) and the species *R. solitarius* (p. 219).

Meristics.

Particular emphasis was placed on meristics, as the numerical characters are in general precisely determinable, free of changes with age, and readily subject to analysis. Meristics provide some of the most striking differences between the isolated populations.

Furthermore, the abundance of material of relatively uniform genetic constitution has offered a favorable opportunity to determine the extent of variability in the meristics of some structures, particularly of fin-ray and gill-raker numbers. The extent of variation determined is surprising, and raises the question that we do not solve, but do present data for solution, as to whether such factors as limited predation and inbreeding in the highly localized populations may have led to increased variability. The unexpected degree of variation in the number of caudal rays (p. 86), for example, opens up this problem.

Moreover, the presumed and apparent genetic integrity of the highly localized populations, some inhabiting a single spring, provide unusually fortunate material for testing some of the basic interrelationships between the numbers developed in different structures, for example: the correlations between the numbers of dorsal and anal rays, between the numbers of pectoral and pelvic rays, and between the numbers of left and right pectoral and pelvic rays. A special point is the determination in such propitious material of the degree of asymmetry and the degree of dextrality in the number of rays in the left and right paired fins, along the lines developed by Hubbs and Hubbs (1945). Data on such relations are presented in the following discussion of the meristics of different structures.

A shadow of uncertainty is always inherent in the use of meristic characters in taxonomy, and in variational analysis, by the circumstance that some of the variation in the numbers of serial parts may be the direct effect of the environment. This is one of the cogent reasons why an experimental approach should be added in the study of such problems as we are now treating. Since environmental temperatures are a major factor known to affect the serial numbers, we have made one approach, albeit rather crude, to evaluating whether the observed differences may be genetically fixed by correlating the determined mean values with the temperatures found in the habitats—a procedure that is especially applicable in spring waters, which tend to be unusually constant in temperature. No obvious correlation was noted for any of the 3 cyprinid species studied, nor was

TABLE 5. *Correlation between mean number of fin rays and of vertebrae (V) and observed summer water temperature of habitats sampled for populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Location	°C[2]	D	A	P_1	P_2	V_p	V_c	V_t
Coils Creek (R6)	13.9	7.77	7.00	13.64	7.79	19.85	17.44	37.50
Crescent Valley (R1)	17.2	7.88	7.00	13.84	7.97	19.76	18.14	37.90
9.5 mi. S. of Wells (R10)	17.2–17.8	7.77	6.98	12.49	6.95	20.31	16.69	37.00
Grass Valley (R9)	18.9	8.09	7.05	12.65	7.18	19.97	16.51	36.49
Warm Spr., Clover V. (R11)	19.3	7.93	7.00	12.72	6.96	20.05	17.37	37.55
Carico L. Valley (R0)	20.6	8.0?	7.0?	12.3?	7.8?	20.3?	18.0?	38.5?
Bishop Creek (R2)	21.1–22.2	7.97	7.00	13.83	7.88	18.75	18.06	36.76
Town Creek (R3)	21.7	7.96	6.93	13.65	7.68	19.35	18.23	37.54
Birch Ranch (R7)	22.2	7.86	6.97	13.31	7.22	18.73	17.75	36.63
Independence V. (R12)	25.6	7.94	6.95	12.72	6.97	19.45	17.24	36.68
Big Shipley Spr. (R8)	27.8	7.77	6.86	13.29	7.23	19.56	17.84	37.42
Potts Ranch (R5)	31.7–34.4	8.00	6.98	13.35	7.68	19.26	17.18	36.59
Dianas Punch Bowl (R5A)	37–39.0	8.02	7.04	13.67	7.63	19.00	18.35	37.50

[1] Data graphed as figures 16 and 17.
[2] In the accounts of the Locations the temperatures have been rounded to the nearest degree. The temperatures for the three lots from Dianas Punch Bowl Springs were taken in February, and the data for this locality are not graphed in figures 16 and 17.

any indicated by analysis of the available data for the vertebrae and fin rays of the several subspecies and races of *Rhinichthys* (table 5; figs. 16, 17).

FIN RAYS. The rays were counted under appropriate magnification and illumination, according to the methods standardized by Hubbs and Lagler (1964, pp. 19–21).

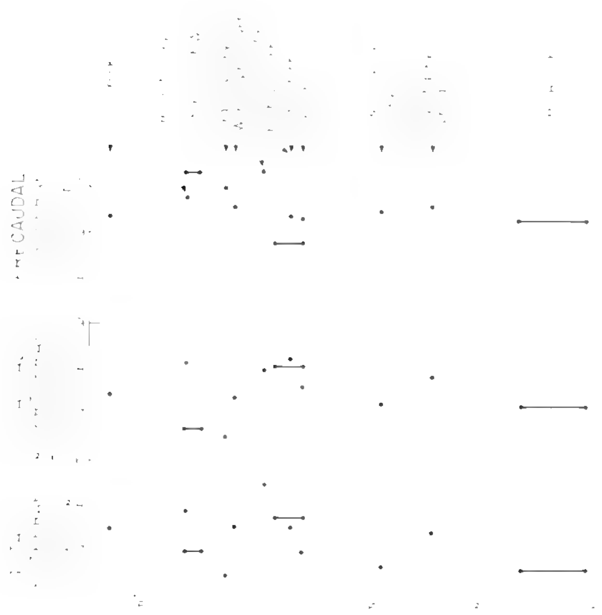


FIGURE 16. Apparent lack of any definite correlation between mean number of vertebrae and recorded water temperatures for 12 populations of *Rhinichthys osculus* from basins in Nevada. Data specified in table 5.

As noted below, in the discussion of vertebral numbers, there seems to be no significant correlation between the number of fin rays and the temperature of the spring-water habitats (fig. 17), strongly suggesting that ray numbers are not determined by the ambient temperatures.

DORSAL AND ANAL RAYS. The count of dorsal and anal rays is of principal rays, and no complication arose as to the first ray to be enumerated, which was always unbranched and essentially of full length. The last two serial elements were consistently counted as one ray, even though, occasionally, they were largely conjoined, or the last element was a minute rudiment. Such conditions are especially frequent when the ray number is higher than the norm. Conversely, when the number is low, the second element of the last ray is often so far removed from the first unit as to simulate what might be interpreted as a non-doubled last ray.

The number of dorsal rays (tables 15, 29, 41) is sharply modal at 8 in all populations of all 3 species under detailed treatment, as it is in a large proportion of small American cyprinids. The observed variation is only 7–9 in *Rhinichthys osculus* and 7–10, with counts of 9 and 10 extremely rare, in *Gila bicolor* and in *Relictus*

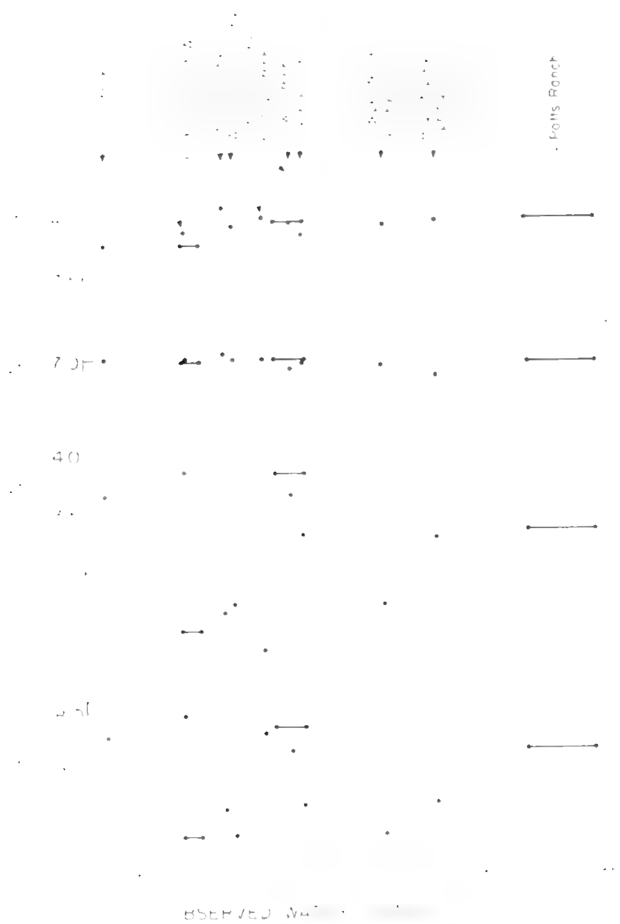


FIGURE 17. Apparent lack of any definite correlation between mean number of fin rays and recorded summer water temperatures for 12 populations of *Rhinichthys osculus* from basins in Nevada. Data specified in table 5. The recently obtained supplementary data for Dianas Punch Bowl Springs, for recorded temperatures of 37–39.0° C., deviate from those for Potts Ranch as follows: dorsal, +.02; anal, +.06; pectoral, +.32; pelvic, –.05.

solitarius. The occasional variants are more often down than up in *Rhinichthys* and *Relictus*, but this is not consistently true for *Gila* and is not true for *Rhinichthys osculus reliquus*.

The anal rays (same tables) are sharply modal at 7 in all the populations of *Rhinichthys osculus* and *Relictus solitarius*, both of which usually inhabit springs and small creeks, but deviate in the *Gila bicolor* populations from the more usual 8

TABLE 6. *Correlation between numbers of dorsal and anal rays in selected samples of cyprinid fishes in the north-central Great Basin.*

	No. of dorsal rays	No. of anal rays			
		5	6	7	8
Rhinichthys osculus robustus:	7	1	5	20	—
5 Locations, L. Diamond system	8	—	4	223	4
	9	—	—	2	4
Rhinichthys osculus reliquus:	7	—	—	2	—
L. Gilbert system	8	—	5	65	6
	9	—	—	7	3
Gila bicolor newarkensis:	7	—	—	11	—
3 Locations, L. Newark system	8	—	2	117	14
	9	—	—	7	—
Relictus solitarius:	7	—	1	7	—
6 Collections, whole range	8	—	5	98	2
	9	—	—	1	—
	10	—	—	1	—

toward or to 7 in the 3 subspecies restricted to springs. Thus the trend toward reduction in counts in spring-inhabiting populations is illustrated. The observed ranges are 5–8 for *Rhinichthys osculus*, 6–9 for *Gila bicolor*, and 6–8 for *Relictus solitarius*.

The numbers of dorsal and anal rays were found to be essentially independent characters, for the positive correlation between these values is at most very low (table 6), as is usual for dorsally and ventrally located structures that are not directly opposite.

CAUDAL RAYS. Even though the caudal rays seem to vary extraordinarily in number in all three species dealt with (table 7), the outermost-marginal of the principal rays (the ones counted) were always extra-wide and unforked. Occasional lack of branching of an inner ray was disregarded. Seemingly interpolated, generally weaker than average rays were counted, even though isolated in the fin membrane (but these did not give rise to the counts of 20 or 21). Occasionally two caudal rays were more or less fused, yet were counted separately, to give, ordinarily, the modal number (19).

The caudal rays in all three species are sharply modal at 19, as expected, for this is the number that is characteristic of the family Cyprinidae through-

TABLE 7. *Number of caudal rays in all populations of each native cyprinid fish treated.*[1]

	Number of principal caudal rays									
	14	15	16	17	18	19	20	21	No.	Mean[2]
Rhinichthys osculus	1	—	1	5	49	450	25	4	535	18.93
Gila bicolor	—	—	1	3	22	329	12	—	367	18.95
Relictus solitarius	—	—	1	3	8	82	8	2	104	18.95

[1] Data from tables 15, 29, 41.
[2] Mean for summarized counts

out its range, and of most other malacopterygian fishes. Because of this consistency, and because the relatively recent trend to count caudal rays is showing that the number of rays in normally forked caudal fins is generally constant within whole families of fishes, it is amazing that a wide range of individual variation, remarkably similar in pattern, has been encountered in all three species (table 7): 16–21, with one aberrant count of 14, in *Rhinichthys osculus*; 16–20 in *Gila bicolor*; and 16–21 in *Relictus solitarius*. This wide fluctuation is wholly age-independent, and does not seem to be population-dependent, for the modality at 19 is so strong and constant, and nearly all of the individual populations display variation in the number (tables 15, 29, 41). Maximum observed ranges for single samples are 5 rays in one sample, and 4 rays in 5, of the 13 samples, in *Rhinichthys*; 5 rays in 1 sample and 3 rays in 5 samples (out of 11) in *Gila*; and 4 rays in 5 of the 6 categories for *Relictus*. There seems to be a greater tendency to decrease than to increase the count. The decrease can occur within a caudal lobe. One *Rhinichthys* specimen had the third and fifth rays from the lowermost so extremely slender as to be detectable with difficulty. The mean number of rays is almost identical in the three species. It is queried above whether this rampant individual variation in a character normally constant may be related to the population structure of these isolated-spring fishes. There is no indication that any of the spring-limited forms exhibits an increased trend toward a decrease in caudal-ray number, despite a weakness of the fin. However, perhaps in correlation with life in very restricted springs, a much greater reduction has been found to characterize a notably dwarfed form of the *Rhinichthys osculus* complex that lives in very small springs in Snake Valley in the Bonneville basin (immediately east of the area under treatment).

PAIRED-FIN RAYS. Pectoral and pelvic rays were all counted, without regard to branching or size, even though the lowermost (innermost) ray was so extremely minute that strong magnification and optimal lighting were required for its perception.

The pectoral rays fluctuate widely in number in all three species, probably in correlation with the moderately high number of rays and the sharp reduction, often to obsolescence, of the rays toward the lower margin of the fin. In any one of the populations herein treated, the usual range is 2–4 rays, and the total range observed within a species is 8 rays (9–16, very rarely fewer than 12) in *Rhinichthys osculus* and in *Relictus solitarius*, and 7 rays (13–19) in *Gila bicolor* (tables 15, 30, 41). There is no consistent interpopulation variance in the populations studied of either *Gila* or *Relictus*.

The three recognized isolated endemic subspecies of *Rhinichthys osculus* (table 15, fig. 18) have a somewhat reduced average number of pectoral rays (12.49–12.72 *vs.* 13.29–13.89 in *R. o. robustus* with an exceptional average of 12.3, based on three specimens from Carico Lake Valley). In contrast, the three recognized isolated subspecies of *Gila bicolor* (table 30, fig. 19) have a slightly higher average (unweighted mean, 16.40) than the populations retained in *G. b. obesa* (unweighted mean, 15.71). The respective ranges of means are 15.88–16.71 and 15.30–16.27. The means (13.48–14.17) are low in *Relictus* (table 41), in comparison with those (15.30–16.71) in the *Gila* samples. Thus, the trend toward reduction in meristic numbers in the isolated spring populations, which are usually dwarfed, is only partially confirmed.

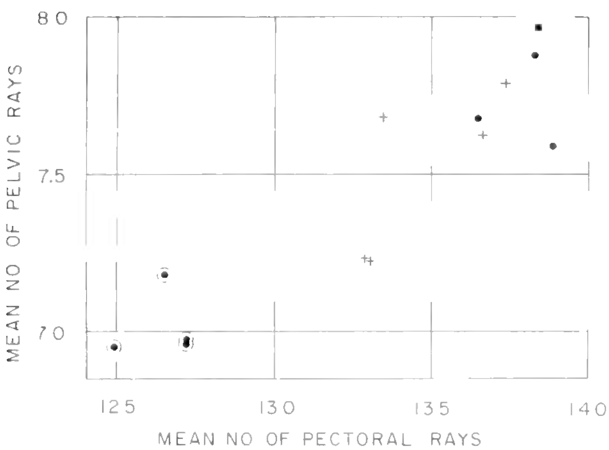


FIGURE 18. Positive correlation, between populations of *Rhinichthys osculus*, in the mean numbers of pelvic and pectoral rays. Entries for isolated endemic subspecies are circles; those for populations from the Diamond Valley system are crosses; those for populations from the Humboldt River system (one introduced into Ruby Valley) are unringed black dots. Data from table 15.

FIGURE 19. Low mean number of pelvic rays associated with high means for pectoral rays in populations of *Gila bicolor*. Lone dots represent collections from Humboldt River system; crosses, those of Diamond Valley system; encircled dots, isolated subspecies. Data from table 30.

The pelvic rays number 5–9 in the *Rhinichthys* samples (table 15) and 6–11 in the *Gila* populations (table 30), with a strong tendency toward reduction in modal number in each species in the races and subspecies confined to spring waters: from 8 to 7 in *Rhinichthys* (fig. 18) and from 9 to 8 in *Gila* (fig. 19). In *Relictus* (table 41) the observed variation is 5–9, but the mode is sharply and consistently at 8.

The mean numbers of pectoral and pelvic rays are strongly correlated positively between populations in the pooled *Rhinichthys* samples, primarily because there is a reduction in the means for each fin in the isolated spring subspecies (fig. 18). In the *Gila* populations, in direct contrast, there appears to be some interpopulation negative correlation between the pectoral-ray and the pelvic-ray numbers (fig. 19), because the isolated differentiated races tend to have a slightly increased pectoral-ray count, along with a markedly reduced number of pelvic rays. No significant correlation is shown in this respect by *Relictus*, because there is little fluctuation in ray number in each fin.

Within populations, however, the positive correlation between the numbers of pectoral and pelvic rays is at most extremely slight. For *Rhinichthys* a positive correlation ($r = 0.39 \pm 0.06$) is very slightly suggested for the combined data for the populations of the Diamond Valley drainage (table 8), but the interpopulation correlation may be at least partly responsible. Similar correlation tables for four subspecies of *Gila bicolor* (not here reproduced) show a similar, extremely slight, far from certain, indication of positive correlation: $r = 0.26 \pm 0.13$ for the

TABLE 8. *Correlation between numbers of rays in both pelvic and both pectoral fins in all four populations of* Rhinichthys osculus *in the Diamond Valley drainage system* ($r = 0.39 \pm 0.06$).

Total pelvic rays	Total pectoral rays							
	24	25	26	27	28	29	30	31
12	1	—	1	-	—			—
13	-	—	—	—		—	—	—
14	10	12	39	9	18	4	1	—
15	1	—	12	5	16	1	3	1
16	1	5	30	12	41	9	13	1
17	—	—	—	—	1	—	1	—
18	-	—	—	—	1	—	—	—

TABLE 9. *Bilateral variation in number of rays in paired fins of cyprinid fishes in the Great Basin in Nevada.*

	Total number counted	Count higher Left L	Count higher Right R	Asymmetry index[1] 100(L+R) / N	Dextrality index[1] 100 R / L+R	100 P[1]
Pectoral counts						
Rhinichthys osculus[2]	503	51	80	26	61	1.1
Gila bicolor[3]	365	55	50	29	48	62
Gila bicolor[4]	308	50	48	32	49	84
Relictus solitarius[5]	115	15	14	25	48	65
Pelvic counts						
Rhinichthys osculus[3]	727	47	42	12	47	60[7]
Rhinichthys osculus[4]	929	76	51	14	40	2.6
Gila bicolor pectinifer[6]	409	43	15	14	26	0.02
Gila bicolor[3]	1884	182	112	16	38	0.00
Gila bicolor[4]	668	73	53	19	42	7.5
Relictus solitarius[5]	229	20	12	14	38	16

[1] Methods of computation and presentation based on Hubbs and Hubbs (1945).
[2] Original data, based wholly on material herein reported.
[3] Data from Hubbs and Hubbs (1945, pp. 274–276); material slightly overlapping that listed in the next line
[4] Based wholly on material herein reported, partly overlapping that reported by Hubbs and Hubbs
[5] Based on representatives from all basins.
[6] Data from Hubbs and Hubbs (1945, pp. 276–277), based on a single collection from Walker Lake, Nevada; not included in material used for next two lines.
[7] Value corrected for 100 P.

Lovelock sample of *G. b. obesa*, 0.27 ± 0.14 for the sample of *G. b. newarkensis* from near Diamond Peak, 0.24 ± 0.17 for *G. b. euchila*, and 0.27 ± 0.19 for *G. b. isolata*. A low degree of positive correlation ($r = 0.23 \pm 0.09$) is shown by the pooled data (also not here reproduced) for *Relictus solitarius*.

All of the data for the pectoral and pelvic rays in the material treated in the present report indicate very high positive correlation between the number of rays on the left and right side, with, as usual, a strong tendency for deviation from partner to increase in frequency with deviation from the mean value of the population, and to diverge from the partner in the direction of the mean value—all in line with the general rules.

An analysis of asymmetry in the ray number of the paired fins (table 9), in the same material, indicates that among specimens with an asymmetrical count the average may be statistically higher on one side than on the other, in line with the exposition by Hubbs and Hubbs (1945: methods of calculation and expression on pp. 232–233; comparable material on pp. 263–277). For the pectoral-ray counts, a slight tendency toward dextrality is indicated for the pooled data on all of the *Rhinichthys osculus* subspecies treated, but no significant deviation from symmetry is evident for the subspecies of *Gila bicolor* or for *Relictus solitarius*. For all three genera, the data for pelvic rays indicate sinistrality (that is, higher counts statistically the more frequent on the left side). The evidence is conclusive for the pooled data on *Gila bicolor*, but somewhat less so for *Rhinichthys osculus* and not of high statistical significance for *Relictus*. Previous data, based in part on the same material (Hubbs and Hubbs, 1945, pp. 276–277), is confirmatory for *Gila bicolor*, but shows statistically untrustworthy sinistrality for *Rhinichthys osculus*. Possibly, the trend toward sinistrality may be somewhat race-dependent. The index of amount of asymmetry seems to be remarkably consistent for the three species treated, ranging in all three, for pooled data, from 12 to 18 percent for the pelvic-ray data and from 25 to 32 percent for the pectoral-ray data. The higher index of asymmetry for the pectoral fin probably reflects in part the higher absolute number of rays.

The observations on bilateral asymmetry in

the paired fins of all three species studied conforms with the principle, first worked out and demonstrated for *Leptocottus armatus* (Hubbs and Hubbs, 1945, pp. 266–272, fig. 1), and since found to hold universally, for both pectoral and pelvic fins, that, when the counts differ on the two sides, the lowest (innermost) and presumably last-formed ray of the fin with the higher ray number is shorter (and generally weaker) than the corresponding ray on the opposite fin. Comparison showed that with very few exceptions this condition holds for the fishes under treatment. For the counts that carried the pertinent notation on the data sheets, the lowest ray in the paired fin having the higher count was shorter than the lowest ray in the opposite fin, of seemingly equal length, or longer, in the following ratios: for the pectoral fin, 83:1:2 for *Rhinichthys*, 73:0:1 for *Gila*, and 16:0:0 for *Relictus*; and for the pelvic fin, 93:0:1 for *Rhinichthys*, 72:0:0 for *Gila*, and 16:0:0 for *Relictus*. The principle now seems to be soundly established, not only for numbers of rays in the paired fins, but also for numbers of parts in various other bilaterally paired meristic structures.

VERTEBRAE. The general availability of high-grade X-ray equipment in ichthyological laboratories is leading to the extensive use of vertebral numbers (and other osteological characters) in fish taxonomy (Miller, 1957). To test for possible differences in vertebral numbers, samples from each of the populations of each of the three species under treatment were X-rayed. Counts were obtained and recorded for the total numbers (tables 16, 31, 42), including the entire hypural plate as 1 and the Weberian apparatus as 4 (the fifth vertebra, following that apparatus, was readily identified by its essentially normal centrum and strong neural spine). Because of variations in the length, strength, and arrangement of the hemal spines and the interhemals near the junction, the distinction of precaudal and caudal vertebrae was perhaps somewhat subjective, and was abandoned for *Gila* and *Relictus*, which, furthermore, showed no sharp differences in the ratio between the numbers in the two sections, but was retained for *Rhinichthys*, for which the distinction seemed less difficult and some average differences appear for each section (table 16). Counts were disregarded whenever the radiograph showed any marked abnormalities, or when (infrequently in some populations), any of the neural or hemal spines were doubled on one or more of the posteriormost caudal vertebrae (it might have been better, and in line with some practice, to have enumerated the centra, without regard to any doubling of the spines). Within each species, inter-population differences in vertebral number are rather limited; there is some overlap between all possible pair combinations. There is also a wide overlap in the total numbers for the samples of each species: 35–40 for *Rhinichthys*, 37–42 for *Gila*, and 35–39 for *Relictus*. The means are consistently lower than 38.0 for *Rhinichthys* (except for the 3 specimens from Carico Lake Valley) and for *Relictus*, but are higher than 38.0 for *Gila*.

Because correlations, on both phenotypic and genotypic basis, have often been found between vertebral numbers and the environmental temperature, and since the habitats of *Rhinichthys osculus* throughout the area studied vary from cold springs to hot springs, the mean total number of vertebrae has been graphically compared with the temperature of the water at the time of collecting (fig. 16). The temperature readings though isolated are presumably representative of basic differences, because all (except those for the samples from Dianas Punch Bowl) were taken during the warm part of the year in spring-fed waters. No evident correlations appear in the graph. Possibly, in reponse to adaptational adjustments to secure normal development at different temperatures, similar meristics have been attained in waters of quite different temperatures.

For *Gila*, the mean vertebral numbers for the 7 stations with recorded temperatures of 20.0° to 23.3° C. ranged from 38.50 to 39.86, with the two extremes at 20.0° C.; the springs designated as "cold," "cool," and "just under luke-warm"

yielded fish with averages of 39.07, 38.39, and 38.78, respectively; the Location with the highest recorded temperature did have the lowest vertebral mean, 38.23, but this collection (Warm Springs in Independence Valley) harbored *G. b. isolata*, the most dwarfed of all the populations, and low counts are often encountered in dwarf forms.

For *Relictus* the mean vertebral numbers ranged from 36.05 to 37.08, with a slight indication of lower values at the warmer Collections: 5 means for Collections at about 12° to 18° C. averaged 36.71; 2 means for Collections with temperature records ranging so as to overlap the two other sets averaged 36.46; and 3 means for Collections at 21° to 25° averaged 36.32. The slight correlation may be fictitious, for the two extreme temperatures were for Collections (7 and 11) rather close together in the same drainage region.

A similar plotting of average numbers of dorsal, anal, pectoral, and pelvic rays of *Rhinichthys osculus* (of all three subspecies) against the recorded spring-water temperatures (fig. 17) showed the same essential lack of correlation, nor was any correlation noted for the data on *Gila bicolor* or *Relictus solitarius*. It therefore seems probable that the local variations in ray numbers are also not attributable to the direct effect of the environmental temperature.

SCALE ROWS. A total of 12 different sets of scale counts were utilized, 4 for *Rhinichthys*, 11 for *Gila*, and 5 for *Relictus*. Irregularities of rows and the frequent incomplete development of the lateral line led to the deleting, for *Rhinichthys* and *Relictus*, of 3 sets of counts, for rows above and below the lateral line, and the total number. To replace the usual counts "above lateral line" and "below lateral line," counts were taken in *Relictus* between the origins of the dorsal and anal fins. In *Gila* only, scales were enumerated in a series, "lateral line to pelvic," running upward and forward from the pelvic-fin insertion to but not including the lateral line.

The methods of counting are those specified by Hubbs and Lagler (1964, pp. 22–23). The "circumference scale count" and "caudal peduncle scale count" of that treatise are here abbreviated to scale rows "around body" and "around peduncle," respectively. In addition to the total count in each of these two sets, separate enumerations were made in *Gila* of the scales in those circumferential counts that lie respectively above and below the lateral line. The two lateral-line rows are added to yield the total-circumference count.

In *Gila*, the scale rows are relatively regular, so that the enumerations are subject to little doubt or subjective interpretation. In some forms of *Rhinichthys* and in *Relictus*, however, some of the counts are approximations, because the scales are more or less deeply embedded, poorly imbricated, and covered by mucus, and are small, often irregularly seriated, and subject to considerable loss and regeneration. Attempts to scrape off excess mucus often results in descaling the body. Undue fluctuations in counts by reason of such circumstances were largely overcome by adopting appropriate magnification and illumination and by using a fine jet of compressed air.

Most of the scale counts enumerated for *Gila* were made for us, using our methods, by a research assistant, John T. Greenbank, in 1942–43. The more difficult counts, those for the two other genera, were all made by one of us (R.R.M.), to help assure uniformity.

All three species vary considerably in scale counts. For the four sets of counts available for all 3 species, using pooled data (table 10), *Rhinichthys* is generally the most variable and *Relictus* seems to be the most constant (but fewer specimens of the latter were counted).

There are some marked differences between populations of *Rhinichthys osculus* and *Gila bicolor* in numbers of scales in the several rows (tables 18 and 32). For example, the Independence Valley subspecies, *Rhinichthys osculus lethoporus* and *Gila bicolor isolata*, differ almost consistently from the other subspecies of each species in nearly all scale counts. Interpopulation

TABLE 10. *Over-all variation in scale counts of the 3 species of Cyprinidae in the north-central Great Basin.*

	Range of values for populations counted		
	Minimum	Mean	Maximum
Lateral-line series			
Rhinichthys osculus (239)[1]	50–66 (17)[2]	56–71 (16)	60–75 (16)
Gila bicolor (260)	42–52 (11)	47–57 (11)	50–64 (15)
Relictus solitarius (75)	50–59 (10)	54–63 (10)	55–70 (16)
Predorsal rows			
Rhinichthys osculus (235)	26–40 (15)	30–43 (14)	35–47 (13)
Gila bicolor (249)	22–28 (7)	27–31 (5)	29–34 (6)
Relictus solitarius (65)	27–32 (6)	31–34 (4)	33–39 (7)
Around body			
Rhinichthys osculus (211)	48–60 (13)	54–67 (14)	60–76 (17)
Gila bicolor (249)	40–51 (12)	44–56 (13)	49–63 (15)
Relictus solitarius (65)	52–60 (9)	55–63 (9)	58–66 (9)
Around peduncle			
Rhinichthys osculus (215)	26–32 (7)	30–36 (7)	31–40 (10)
Gila bicolor (249)	20–29 (10)	25–32 (8)	28–35 (8)
Relictus solitarius (65)	28–32 (5)	29–33 (5)	30–34 (5)

[1] These numbers in parentheses after the species names indicate the number of specimens counted for the stated scale row.
[2] Numbers in parentheses indicate the range in counts for the minimum, mean, and maximum values recorded for each species

differences in *Relictus solitarius* in scale counts are less striking (p. 223, table 43).

Lateral-line pore counts are discussed above.

GILL-RAKERS. The raker count, often made on both sides represents the total number on the outer face of the first arch, including the few at and just above the rounded angle. With due care, the numbers can be ascertained with high precision and repeatability. We use appropriate magnification, adequate illumination, and a fine jet of compressed air. It is imperative that all rudiments at each end of the series be included, because slight rudiments grade into well developed rakers. In the cyprinids studied, unlike clupeids and some other fishes, we have found that specimens as short as 30 mm. had attained the full numerical complement of rakers, so that such small specimens could be safely counted as representative of the species.

In the populations studied, the rakers varied widely in number. In *Rhinichthys* and *Relictus* the wide variation, from 5 to 10 and from 7 to 12, respectively (tables 18, 43), is consistent with the principle that degenerate structures tend to be highly variable. The vastly greater total fluctuation, from 8 to 40 for the whole complex that we treat as a single species, *Gila bicolor*, and the concomitant variation in size, texture, and structure, is attributable to trophic divergence (pp. 146–147).

Counts only were considered for the populations of *Rhinichthys* and *Relictus*, for in these genera the rakers are consistently few, short, fleshy, and weak, but for the populations of *Gila bicolor* consideration was also given to degree of development. In that species, in apparent trophic adaptation, as in many species or species groups of fishes, the rakers diverge widely in size, texture, and structure (fig. 28), as well as in number. Some of these differences are appreciable by inspection, and are subject to description. For quantification of length, we utilized the length of the longest raker (usually readily selectable by inspection), which lies slightly below, or rarely at, the angle. The left arch was consistently counted. The measurement has been obtained with precision dial calipers marked in 0.1 mm. intervals and estimated to 0.01 mm., with an error of probably less than 0.05 mm. One point of the calipers was pressed lightly against the, often more or less concealed, hardened base of the raker. Since a graph showing raker length plotted against standard length demonstrated an essentially straight-line relation between those parameters,

the raker lengths were tallied as permillages of the standard length. Because of differences between races in proportionate head length, raker lengths were also tallied against head length. Between, and more loosely within, populations, there is, in *Gila bicolor* (see p. 146 for details), roughly, a positive correlation between number of rakers and their size (fig. 29) and between number and form.

Another special aspect of the meristic analyses has been the determination of the correlation within the *Gila bicolor* complex (whether we call these forms subspecies or species) between numbers of gill-rakers and of pharyngeal teeth (p. 145; table 24), as an approach to the analysis of introgression (pp. 144–147) between the lacustrine form (*pectinifer*) and the fluviatile form (*obesa*). Much variation has been found in numbers of both gill-rakers and teeth in populations of *Gila bicolor* that show evidence of past hybridization between those forms (p. 145).

Pharyngeal teeth. Numbers of pharyngeal teeth have traditionally been emphasized in the classification and nomenclature of cyprinid fishes, but few studies have assessed the degree of individual variation or have critically tested the value of the observed patterns. In this study, more than the usual casual attention has been accorded to variation in the number and arrangement of these teeth. Large series of discrete populations have provided appropriate material for this study.

In determining the number of the teeth, it must be kept in mind that individual teeth are frequently lost in the normal process of tooth replacement and sometimes in the extraction of the arches (which calls for care, experience, and skill). Loss of teeth must be evaluated by recognition of the alveoli, which need be differentiated from nerve and blood-vessel perforations (see fig. 45). Ordinarily, alveoli are larger, are rimmed, and follow the pattern of tooth arrangement.

Difficulties in counting increase with the age of the fish; because in old fish the teeth are not always replaced, margins of the arch may become eroded, and the alveoli may become more or less closed with bony tissue. Younger fish seldom show such modifications, and are therefore preferable for counting, and for the study of arch and tooth structure. With good tools, care, and practice, arches can be extracted from even extremely small fish, without damage to arch or body.

One of the surprising and unexpected finds in the present study is that the number of teeth in the main (morphologically outer) row is occasionally reduced to 3 in all three genera studied (pp. 97, 148, 190). It was long assumed that the only modern North American cyprinid having only 3 teeth (in this case normally on both sides) is a peculiar genus and species, *Stypodon signifer* Garman, which occupied an endorheic basin in northern México but is now probably extinct (Miller, 1961, p. 380). The occasional reduction of the tooth number to 3 on the right side of any North American cyprinid was apparently first recorded by Miller (1945a) in describing dental variation in *Snyderichthys* (now *Gila*) *copei* (Jordan and Gilbert), in which a syntype of *Squalius aliciae* yielded a formula of 2, 4—3, 2 and a specimen of *G. copei* from Little Wood River, Idaho, had a formula of 1, 4—3, 1. This deviation was also noted by Hubbs and Hubbs (1958, pp. 299, 303), in the original description of another cyprinid of northern México, *Notropis saladonis*. Overlooking the reported variants of *G. copei*, and also *Stypodon*, Lachner and Jenkins (1967, p. 577) stated that reduction to 3 teeth had been found, among North American cyprinids, only in *Notropis saladonis* and in *Nocomis leptocephalus* (Girard); in the latter they noted occasional reduction to 3 on one or both sides. We have found the teeth in *Agosia chrysogaster* Girard to vary in one specimen from the normal complement of 4—4 to 3—4 (an exception to the general rule of having the higher number of teeth on the left side; similarly, we have found in *Gila bicolor*, rarely, variants with 3—4 or 4—5 teeth). In *Aztecula vittata* (Girard), from the Valley of

México, rare variants from the 4—4 norm are 3—4, 4—3, and 5—4 (1 each).

La Rivers (1962, p. 427, fig. 196) figured a pharyngeal arch of *Rhinichthys osculus nevadensis* Gilbert as toothless and stated that the dentition of this form "varies from no teeth (0—0/0—0) to the following combinations—0—1/3—0, 0—3/1—0 and 0—1/0—0," obviously on the basis of damaged or diseased arches.

The occasional increase in the number of teeth in the main row beyond 5, to 6, was noted twice in a sample of *Gila bicolor obesa*. Evans and Deubler (1955, p. 32) reported 6 teeth in the main row in a specimen of *Semotilus atromaculatus* (Mitchill). It has generally been thought that the number is increased beyond 5 in only one North American cyprinid genus, *Orthodon* (of the Sacramento River system).

Snyder (1917, p. 62) noted that "*Siphateles obesus*" (as he called the stream form) usually has 5 teeth on the left arch and 4 on the right, and Hubbs and Hubbs (1945, pp. 284–285) generalized that those cyrinids that are bilaterally asymmetrical in pharyngeal-tooth number have the higher number on the left arch. Both prior and subsequent observations have solidified this conclusion. For other species of *Gila*, Hubbs and Miller (1943, p. 356), Miller (1945b, p. 107; 1963, p. 23), and Miller and Hubbs (1962, pp. 112–113) have found the teeth in the main row to be almost always 5—4 (following convention in listing the left side first). Evans and Deubler (1955, p. 32) stated that all 150 specimens counted of *Clinostomus elongatus* Kirtland have 2, 5—4, 2 teeth.

Exceptions to the rule that the count on the left side, if different, is the higher, are provided by individual variants only. The only contrary statement found in the literature is that by Chu (1935, p. 107), who stated that "*Phoxinus* . . . . has the teeth on the right side constantly 2, 5 while those on the left side are 1 or 2, 4 or 5 (0, 1 or 2, 4 or 5/5, 2, 0)." However, in the same treatise (p. 116) he gave the formula as "2, 5/4 or 5, 1 or 2" for *Phoxinus lagowskii variegatus* Günther and figured (pl. 22, fig. 105) a right arch with 4, 2 teeth. *Phoxinus phoxinus* (Linnaeus) is known to agree with other cyprinids in normally having the higher count on the left side (Hubbs and Hubbs, 1945, p. 285). Specimens of *P. phoxinus* and *P. percnurus* (Pallas) examined by us have 5—4 teeth in the main row. Obviously, Chu's statement was a *lapsus calami*.

In the material under treatment of all three genera and species, the higher number of teeth in the main row is on the left side. In *Rhinichthys osculus* the only variant formulae from the normal 4—4 among 79 specimens are 5—4 in two and 4—3 in one. In *Gila bicolor*, among the great majority having bilaterally asymmetric counts, the only variants from 5—4 are 6—4 in two, 4—3 in one, and, as a reversal of laterality, 4—5 in only three fish (table 23, p. 149). In *Relictus solitarius*, among 75 specimens counted, the only variants from 4—4 are 4—3 and 5—4, each in two fish.

The remarkable constancy in the number of pharyngeal teeth on each arch seems to be relatable to the individual specialization of the teeth, which is indicated by the regular sequence of replacement (Evans and Deubler, 1955) and by the distinctive size and form of the particular teeth. This distinctiveness was observed in all three species, but may be illustrated by the notations made for *Gila bicolor*. The first (uppermost and posteriormost) tooth is long and very slender. In some specimens it is crowded to the outer side (that is, toward the concavity of the arch), where it is closely juxtaposed against the second tooth. That tooth is usually also very slender. The third tooth is much more robust, more compressed, and often the longest. The fourth tooth is usually somewhat shorter, but, on the left side, is also robust and compressed. On the right side, the fourth (and last) tooth is usually much shortened, but wider than the third, and the grinding surface on the fourth tooth is usually less developed than on the preceding teeth, although this tooth usually retains the strong hook. The fifth tooth, normally formed

only on the left arch, is almost invariably a small, pointed peg, well separated from the fourth tooth. Occasionally, however, it ends in a slight to moderate hook and, rarely, it develops a small grinding surface.

For all three species represented in the study area, the data on tooth number is consonant with the generalization that the number of serial elements becomes reduced in populations inhabiting isolated waters. *Rhinichthys osculus robustus*, which is largely confined to springs, normally has only one tooth in the lesser row (p. 97), whereas subspecies inhabiting integrated streams often have two teeth in this row. *Gila bicolor obesa* and its derivatives, which usually occupy springs and small creeks, normally have a dental formula of 5—4, whereas the lacustrine type, *G. b. pectinifer* (Snyder), typically has 5—5 teeth. *Relictus solitarius*, which is virtually confined to springs, normally has 4—4 teeth.

The form of the pharyngeal arch has also been accorded attention, particularly in the generic comparisons (pp. 189–193).

DISTRIBUTION AND HABITAT.

A major phase of the study of the fishes of the isolated waters of the arid American West, specifically of the north-central Great Basin, has been an analysis of the distribution of the remnant fish populations in terms of paleohydrographic history (pp. 70–79). The problems of faunal depauperation, limited sympatry, and correlation between size of area and richness of the fauna are summarized above. Particular distributions of the four genera under treatment, and of the represented species, subspecies, and races, are treated below under the respective headings.

Treated below also, as a characteristic attribute of the several forms and populations, are their respective types of habitat. For each location, attention is paid to the isolation and the size of the habitat; to the abundance of the individual populations, largely in terms of numbers of specimens collected; to the temperature of the spring waters, which tends to be a critical factor (most readings were in the Fahrenheit scale, which have been computed to the nearest degree Celsius); to various other major ecological criteria, such as clarity and other qualities of the water, and the nature of the bottom, current, and vegetation; and to associated fish species, native and introduced. Listed also, when available, is the type of collecting gear ("woven-mesh seine" usually refers to the "Common Sense" type).

Unfortunately, little of the habitat information was quantified by us, and very little was recorded on the widely varying content of dissolved salts, which presumably has been a factor of very considerable importance in the survival or extinction, and probably in the speciation of the populations; hence in their occurrence and distribution. It is unfortunate that systematic analyses have not been run, and studied in relation to the dwindling fish fauna. Prior to undertaking the major expedition of 1938 the senior author made arrangements to have such analyses run in the pollution and water-quality laboratory operated at the University of Missouri by the U. S. Bureau of Fisheries. Water samples were taken at the many springs examined and were dispatched at intervals to that laboratory, but no report was received. Fortunately, a considerable number of analyses have been published for spring waters in the basins under study, for example by Clark and Riddell (1920) for springs in Steptoe Valley, and in the reports of the Nevada Department of Conservation and Natural Resources providing water-resource appraisals of springs in many of the valleys of the state (these reports are referred to in the preceding treatment of the remnant waters of individual basins and/or in the following accounts of the habitats of the several species). It is to be hoped that in future explorations of the area the chemical constitution of the isolated waters, and their other characteristics, will be still further analyzed.

Outstanding features of the habitats of native fishes in the Great Basin are the vast reduction of surface water in which any fish could survive and the limitation of the fish to only parts of the

miniscule supply. In general, the native fishes are confined to valley springs, most of which issue along faults margining the valleys. Though many of such springs are extremely small, at times with virtually no discharge, the water supply tends to be more or less constant, and the very few fishes that have survived, in a small percentage of the basins, have become adapted to withstand the precarious habitats.

The valley springs have been favorable for the survival of remnant fish life not only on ecological grounds but also in terms of long perpetuity. Long existence is indicated not only by the very circumstance of present occurrence, but also by other evidence, such as the extensive accumulation about some springs of travertine deposits and of Indian artifacts, often of varied type and different degree of patination.

As is repeatedly mentioned in the preceding discussions of the remnant fish life for each basin, and in the subsequent accounts of the species, the rather numerous mountain springs and creeks in some of the basins are devoid of native fish life. Introduced fish, especially trout, may multiply and persist, at least for some years, until the hazards of existence become insuperable. In years of great drought the mountain-side and canyon-bottom springs and the canyon streams may become temporarily dry. Furthermore, they are subject to the occasional, even though generally very infrequent, fate of violent scouring by the torrential precipitation that characterizes the desert climate. The fishes are washed out onto the playas, and the waters then subside too abruptly and too completely to allow the fish to return to habitable waters.

Evidence of diminishing waters—in lakes, streams, and springs—strike the eye throughout the Great Basin. The postpluvial changes in climate have obviously been a dominant factor, but indications seem to be increasingly emerging that spring flow has been diminishing even without evidence of climatic change. The vast amount of water that accumulated in aquifers when the pluvial lakes filled large parts of the basins must have continued draining out by springs even after the present climatic conditions became established, and probably even during times that have been drier than the present. The wonder is that even a few fishes have survived in the precarious habitats of the Great Basin.

Structure and Status of Populations.

Attention has been paid to the structure and status of the various localized populations of the three cyprinid species that are native to the north-central Great Basin. Particularly for *Rhinichthys*, the mass random collections have been analyzed to show the distribution of the fish by size and length. It is concluded that *Rhinichthys*, and probably the two other genera, ordinarily spawn in the summer, and that for some weeks the young of the two sexes are about equal in number and in size. As yearlings, females are more numerous and somewhat larger than males, and comprise a much larger biomass. After spawning as yearlings, the males seem to die off or to stop growing, whereas some females appear to live on and continue to grow.

The past, present, and possible future of the populations have also been given consideration. Extensive local questioning, fortunately during the time when observant early settlers were still alive, has yielded evidence on the indigeneity or introduction of species, and on changes in population. The evidence is recounted under the headings of the several forms.

SPECKLED DACE

Rhinichthys osculus (Girard).

This species, one of the four that have persisted in the complex of basins under treatment, is the most ubiquitous freshwater fish in western United States. Uncounted local variants occupy an almost endless number of habitats, ranging from torrential creeks in the major river systems to the tiniest and most isolated spring holes in the desiccated valleys that comprise the Great Basin. Hints of this situation, particularly as it applies to the remnant waters of the arid West, have been

given by us (Hubbs and Miller, 1948b), and others, but the very magnitude of the problem has retarded extensive critical studies. Many of the forms are highly localized. For example, *Rhinichthys osculus thermalis* (Hubbs and Kuhne, 1937) is known from a single warm spring in the Green River basin in Wyoming.

Varying generic treatment has been accorded this species: during the present century it has been referred successively to *Agosia*, to the more restricted taxon *Apocope*, and, currently, to *Rhinichthys*. That genus had previously been restricted to *R. atratulus* (Hermann), which is widespread through eastern United States, and to *R. cataractae* (Valenciennes), which ranges across northern North America from coast to coast, and its derivative, *R. evermanni* Snyder, of the Umpqua River system in Oregon. *Rhinichthys* seems to be the best resting place for this western group, in the present confusion on generic recognition among American cyprinids that appears to approach potential chaos. For the present, we follow Gilbert (1893, p. 229) in referring the group to *Apocope* Cope on the subgeneric level. The supposed generic distinction of *Apocope* on the basis of the continuous rostral groove breaks down, particularly in the Colorado River basin, where in many forms the premaxilla is commonly or even regularly bound down by a frenum. *Agosia*, which has usually been thought to be a closely related genus, occupying Williams and Gila rivers of the lower Colorado River system and tributaries to the Gulf of California farther south, may not be on the same phyletic line and we feel that it should be held separate. Except for two forms of the Columbia River fauna, *R. falcatus* (Eigenmann and Eigenmann) certainly, and *R. umatilla* (Gilbert and Evermann) probably, we currently treat all the many named and still more numerous yet unnamed forms as constituting a single highly varying species, *R. osculus*. Perhaps *R. falcatus* should be separated generically, for it is trenchantly distinct.

Despite the wide range of variation displayed in many characters, in large part related to the type of habitat, and in part to degeneration in isolated springs, the *Apocope* complex is held together by a considerable number of morphological and other features. The multitudinous local forms are all small minnows, rather slender and terete, with the body heaviest well forward, with rounded contours, and with a small eye and small mouth. They are generally rather dark and more or less striped and mottled, and, as the vernacular name indicates, are speckled, because of the blackening of regenerated scales (p. 210). They have rather slimy integuments, and the deeply embedded, more or less irregularly aligned scales are smoothly oval, with no sharp distinction between anterior, lateral (dorsal, ventral), and posterior fields, and with radii well developed around the entire scale (except in *R. falcatus*). There is no horny sheath on the jaws. The lower jaw is included, and the posterior tip of the mandible is not prominent. The small barbel is terminal or subterminal on the upper jaw, but is subject to a varying degree of obsolescence, especially in isolated spring habitats (as is illustrated by the forms herein described as new subspecies). The pharyngeal teeth normally number 1 or 2, 4—4, 1 or 2, but in the Great Basin area seem to be subject to little deviation from the formula 1, 4—4, 1. One variant from this formula, with 0, 5—4, 0 was reported for *R. o. robustus* from Soldier Meadows, Nevada (Hubbs and Miller, 1948a, pp. 16, 17). Schultz and Schaefer (1936, p. 3) indicated that a considerable number of specimens of *Rhinichthys osculus* lack any teeth in the lesser row, but we suspect that they overlooked some alveoli that represent lost teeth. Taking such alveoli into account, we have found, for 79 specimens representing all but one of the populations of *Rhinichthys osculus* herein treated, the formula is 1, 4—4, 1, with these exceptions: 1, 5—4, 1 in two specimens; 1, 4—3, 1 in one; 2, 4—4, 2 in three, and 0, 4—4, 0 in two. Other subspecies commonly have two teeth in the lesser row. The ordinarily single tooth comprising the lesser row in Great Basin forms is almost always rather strong. The teeth are well hooked and the grind-

ing surface is sometimes slightly cultrate and crenate. The arch is relatively strong and sharply curved; its upper arm is weak and very flat. The gill-rakers consistently remain few and short, with no tendency to increase in number or in length in correlation with feeding on plankton—such as has evolved in many cyprinids (and other fishes) throughout the world (Hubbs, 1941b, pp. 187–188). The intestine is short, with a single simple loop in the form of a compressed S, equivalent to the Group 1 type of Kafuku (1958, fig. 7 and pl. 4, 1a). The dorsal fin originates somewhat behind the vertical from the insertion of the pelvic. Typically, the dorsal rays number 8 (except in the Columbia River system), the anal rays almost invariably 7, and the pelvic rays either 7 or 8. In males, the pectoral fin is enlarged in length and width and tends to be arched downward where the several outer rays are markedly thickened, so that the fin is reflected outward and downward along the outer (upper) edge (these characters are exaggerated in breeding males). The nuptial tubercles (fig. 23B) tend to be obsolescent or obsolete on the head and body (not so true in some forms of the Colorado River system), and on the fins are confined to the first several branched pectoral rays, on which the small hooks occur 1 per segment, in a single row, weak basally, but strong where once branched. They are diagnostically lacking on the much thickened first pectoral ray, on all other fins, and on the body (not so restricted in some other subspecies). Though inhabiting a wide range of habitats, particularly in respect to current, the varied forms are ordinarily mainly restricted to smaller waters (creeks and springs) that are neither very highly mineralized nor very warm. Furthermore, they generally avoid lakes, and any pelagic or deep habitat. None of the forms here under treatment have developed enlarged falcate fins and the very slender caudal peduncle that are exhibited by certain local forms that have become adapted to life in consistently rapid water (as is particularly well exemplified in certain tributaries of the Colorado River). Many of these characters seem rather superficial or even subjective, but together they put a stamp on the fish that makes it ordinarily possible to recognize it at a glance as belonging to *Apocope*, despite great variations in several respects.

In so far as checked, the osteological characters throughout the species essentially agree with those assigned to *Rhinichthys* in the account of the genus *Relictus* (pp. 181–193, figs. 38–45).

Included in the subgenus *Apocope* are various forms that until the 1930's were accorded specific rank. For example, Jordan and Evermann (1896, pp. 308–313) recognized in the subgenus *Apocope* the following species (referred generically to *Agosia*): *Agosia oscula, A. yarrowi, A. couesii, A. adobe, A. nevadensis, A. nubila, A. carringtonii*, and *A. velifera* as well as *A. umatilla* and *A. falcata*. All of the forms other than *Rhinichthys umatilla* and *R. falcatus* we have long regarded as conspecific, and for the species we early adopted the name *osculus*, one of three proposed by Girard in 1856 (p. 186) as *Argyreus osculus, A. notabilis*, and *A. nubilus*. The name *osculus* was definitely selected over *notabilis* by Jordan and Evermann (1896, p. 309), by synonymizing *Argyreus notabilis* under *Agosia oscula*, and was formally selected over *nubila* by Schultz (1936, p. 148), through the adoption of the names *Apocope oscula nubila* and *Apocope oscula oscula*. In temporary reversion, following the then accepted but now invalidated principle of the precedence of page and line reviser action over that of selection by first reviser, Miller (1952, p. 30) adopted *Rhinichthys nubilus* in place of *R. osculus* as the species name. The binomen *Rhinichthys osculus* has been adopted by Bailey *et al.* (1960, 1970) for all forms of *Rhinichthys* other than *R. atratulus, R. cataractae, R. evermanni*, and *R. falcatus*.

Local Forms Of *Rhinichthys osculus* In North-Central Great Basin

In the basin area of Nevada under investigation, local forms referred to *Rhinichthys osculus* occupy five springs in the rather extensive pluvial

Lake Diamond drainage basin, a single spring in the pluvial Lake Gilbert basin (recently exterminated), and three springs in the pluvial Lake Clover basin. They also inhabit headwater creeks and springs in the surrounding drainage systems: to the north, the Columbia River; to the east, Lake Bonneville; to the south, the Colorado River; to the southwest, the isolated Lake Toiyabe basin (see p. 15); to the west, the Reese River system, tributary to the Humboldt; and, to the northwest, the basins of the reputedly pluvial lakes Carico and Crescent, which in high flood discharge into Humboldt River. In the present study we defer detailed comparisons with the local forms that occur to the east, south, and west, but have included four samples from the Humboldt River system immediately to the north (including the two valleys just mentioned), as these seem to represent, as nearly as is feasible, the ancestral type that gave rise to the nine native populations discovered in the area of special study. These nine populations occur in three of the six basins that form, within the area of special study, the northern file of now completely enclosed depressions that were once connected with Humboldt River. *Rhinichthys osculus* is not represented in the basin of pluvial Lake Newark, nor in the basins of pluvial lakes Franklin (except by recent introduction), Gale, Waring, and Steptoe, all of which are occupied by only one native fish, the ecologically rather similar relict dace, *Relictus solitarius*.

Altogether, including extraneous samples for comparison and the one introduced stock, 14 populations referred to *Rhinichthys osculus* have been analyzed in the present study. They are here, as on the maps (figs. 1, 3, 8, 12), referred to as representing Locations R0 to R12. The series are referred to 4 subspecies, as follows:

(A) *Rhinichthys osculus robustus* (Rutter):
- From nearby basins discharging in rare floods into Humboldt River:
  - R0, spring in Carico Lake Valley.
  - R1, Indian Creek in Crescent Valley.
- From present headwaters of Humboldt River, near Wells:
  - R2, Bishop Creek.
  - R3, spring near Town Creek.
- Regarded as having been stocked from a Humboldt River headwater:
  - R4, spring in Ruby Valley.
- From springs in basin of pluvial Lake Diamond (not differentiated enough for subspecific separation):
  - R5, hot spring at Potts Ranch, near pluvial Monitor River, below Lake Diana.
  - R5A, hot-spring flow 6 km. south-southwest of R5, at approximate source of any flow of the south branch of Stoneberger Creek.
  - R6, spring flow in Coils Creek (on Three Bar Ranch), a northern tributary of floodwater course representing Monitor River.
  - R7, spring at Birch Ranch, on east side of the bed of ancient Lake Diamond.
  - R8, Big Shipley Spring on west side of bed of same lake.
  - Extensive inquiry and exploration has disclosed no other populations of the species in the basin of Lake Diamond, though some may exist in the immediate vicinity of Big Shipley Spring and/or along the fault to the southward; and there is a report of fish thought not to be young trout in Roberts Creek (p. 19).

(B) *Rhinichthys osculus reliquus* Hubbs and Miller, a very distinct relict (recently exterminated):
- From basin of pluvial Lake Gilbert:
  - R9, a single spring complex on Grass Valley Ranch.

(C) *Rhinichthys osculus oligoporus* Hubbs and Miller:
- From Clover Valley, in the basin of pluvial Lake Clover:
  - R10, a large spring at Wright (formerly Ralph) Ranch, 9.5 miles south of Wells, near northwest tip of the ancient lake.
  - R11, large spring at Warm Spring Ranch, in southwest corner of the old lake bed.

(D) *Rhinichthys osculus lethoporus* Hubbs and Miller:
- From Independence Valley, also in the bed of pluvial Lake Clover:
  - R12, Warm Springs, a cluster on the west side of northern arm of Independence Valley.

In the separation of the subspecies, particular stress is accorded the degeneration of the barbel and of the lateral line. The development of these sensory structures in the forms of *Rhinichthys osculus* under treatment is now discussed.

TABLE 11. *Number and size of barbels in populations of* Rhinichthys osculus *in certain basins in Nevada.*

Subspecies Pluvial lake system Locality	No. of barbels 0—0	 0—1, 1—0	 1—1	Size of barbel (subjectively appraised) Absent	 Minute	 Small	 Large
Rhinichthys osculus robustus							
L. Lahontan (Humboldt R.)							
Carico L. Valley	1	1	1	3	—	3	—
Crescent Valley	13	23	52	49	42	72	13
Bishop Creek	16	2	21	34	9	26	9
Springs near Town Cr.	11	10	19	32	28	17	3
L. Franklin (introduced)							
Ruby Valley	2	2	8	6	4	8	6
L. Diamond							
Potts Ranch	12	11	10	35	18	13	—
Dianas Punch Bowl	6	1	13	13	5	22	—
Coils Creek	13	9	18	35	8	28	9
Birch Ranch	42	10	9	94	17	11	—
Big Shipley Spr.	42	41	46	125	55	77	1
Rhinichthys osculus reliquus							
L. Gilbert							
Grass Valley	199	1	—	399	1	—	—
Rhinichthys osculus oligoporus							
L. Clover							
9.5 mi. S. of Wells	25		—	50	—	—	—
Warm Sprs., Clover V.	26	—	—	52	—	—	—
Rhinichthys osculus lethoporus							
L. Clover							
Independence Valley	75	4	—	154	3	1	—

Development Of The Barbel

In the study of the populations of *Rhinichthys osculus* under treatment, it was found that the barbel often requires close examination to be detected, because it is often lacking, extremely minute, or obscured from external view behind the concealed tip of the maxilla. It usually stems from the lower, far-posterior, outer surface of the maxilla, but in some individuals is on the posterior edge, or hangs from the lower free edge of the maxillary fold, where it may be deeply concealed. Reliable determination requires adequate magnification and illumination, often supplemented by the use of a fine jet of compressed air.

As Snyder (1917, p. 67) indicated, the development of the barbel is subject to much variation between and within populations. As we have pointed out, the barbel, although commonly regarded as a generic character of *Rhinichthys*, is subject to obsolescence in local populations that are restricted to isolated springs. That this is not the direct phenotypic result of living in springs is suggested by the retention of the usual number and size of barbels in a stock recently established in a spring in Ruby Valley as an obvious result of introduction from a headwater tributary of Humboldt River (p. 107). In those headwaters, as well as in the five populations that have persisted in the Lake Diamond system, which we also refer to *R. o. robustus*, the barbel is very frequently retained on one or both sides, though with considerable variation (table 11). The four other populations that have persisted in the basin complex under treatment, and that we refer to three distinct subspecies, always or nearly always lack the barbel on both sides. These subspecies are *R. o. reliquus* of Grass Valley, in the basin of pluvial Lake Gilbert, and *R. o. oligoporus* and *R. o. lethoporus*, of Clover and Independence valleys, respectively, both in the basin of pluvial Lake Clover. The last two subspecies, but not *R. o. reliquus*, are further characterized by a great reduction of lateral-line pores (see below).

In *R. o. reliquus* only one minute barbel, on

TABLE 12. *Number of lateral-line pores at different sizes of fish, and condition of supratemporal canal, in populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Standard length (mm.)	*Rhinichthys osculus robustus* and modified populations										*R. o. reliquus*	*R. o. oligoporus*		*R. o. lethoporus*
	Carico L. Valley	Crescent Valley	Bishop Creek	Springs near Town Cr.	Ruby Valley	Potts Ranch	Dianas Punch Bowl	Coils Creek	Birch Ranch	Big Shipley Spring	Grass Valley	9.5 mi. S. of Wells	Warm Sprs., Clover Valley	Independence Valley
13	— —	0–0 (0.0_{2})	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
14	— —	0–0 (0.0_{6})	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
15	— —	0–0 (0.0_{4})	— —	0–0 (0.0_{2})	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
16	— —	0–0 (0.0_{2})	— —	0–0 (0.0_{2})	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
17	— —	0–0 (0.0_{3})	— —	0–0 (0.0_{11})	— —	— —	— —	— —	0–0 (0.0_{2})	— —	— —	— —	— —	— —
18	— —	— —	— —	0–0 (0.0_{16})	— —	— —	— —	— —	0–0 (0.0_{3})	— —	0–0 (0.0_{4})	— —	— —	— —
19	— —	— —	0–0 (0.0_{23})	0–0 (0.0_{14})	— —	— —	— —	0–1 (0.2_{10})	— —	— —	0–0 (0.0_{8})	— —	0–0 (0.0_{22})	— —
20	— —	0–0 (0.0_{2})	0–0 (0.0_{10})	0–0 (0.0_{28})	— —	— —	— —	0–0 (0.0_{14})	0–0 (0.0_{2})	— —	0–0 (0.0_{4})	— —	0–0 (0.0_{10})	— —
21	— —	— —	0–1 (0.05_{20})	0–0 (0.0_{10})	— —	— —	1 (1.0_{1})	0–0 (0.0_{5})	0–0 (0.0_{4})	— —	0–0 (0.0_{14})	0–0 (0.0_{4})	0–1 (0.03_{20})	— —
22	— —	— —	0–0 (0.0_{4})	— —	— —	— —	1–2 (1.5_{2})	0–1 (0.4_{14})	0–2 (0.7_{4})	0–0 (0.0_{2})	0–1 (0.3_{11})	0–1 (0.5_{2})	0–0 (0.0_{4})	— —
23	— —	— —	1–1 (1.0_{1})	— —	— —	— —	2 (2.0_{1})	0–2 (0.6_{17})	0–1 (0.6_{5})	0–2 (0.7_{4})	0–1 (0.3_{14})	0–1 (0.2_{12})	1–1 (1.0_{4})	— —
24	— —	— —	0–2 (0.7_{19})	— —	— —	— —	9 (9.0_{1})	0–2 (0.9_{8})	1–4 (2.5_{4})	2–3 (2.5_{2})	0–1 (0.7_{6})	0–1 (0.7_{8})	0–2 (0.7_{18})	— —
25	— —	— —	0–1 (1.0_{11})	— —	— —	— —	10–13 (11.5_{2})	1–1 (1.0_{2})	1–12 (4.3_{12})	3–12 (7.1_{9})	0–1 (0.7_{10})	0–2 (0.8_{12})	0–1 (0.9_{14})	— —
26	— —	— —	1–2 (1.7_{6})	— —	— —	— —	2–9 (6.1_{7})	1–3 (1.9_{8})	6–15 (9.0_{6})	4–11 (7.8_{5})	0–1 (0.3_{16})	0–1 (0.9_{8})	1–2 (1.3_{8})	— —

[1] For each indicated size category in each population there is given the range in counts and, in parentheses, the mean number and, as a subscript, the number of counts (both sides usually counted). For method of counting, see p. 81. Means have been graphed (figs. 25, 26).

(Table continued on next page.)

TABLE 12. CONTINUED.

Standard length (mm.)	*Rhinichthys osculus robustus* and modified populations										*R. o. reliquus*	*R. o. oligoporus*		*R. o. lethoporus*
	Carico L. Valley	Crescent Valley	Bishop Creek	Springs near Town Cr.	Ruby Valley	Potts Ranch	Dianas Punch Bowl	Coils Creek	Birch Ranch	Big Shipley Spring	Grass Valley	9.5 mi. S. of Wells	Warm Sprs., Clover Valley	Independence Valley
27	—	—	0–8 (1.9_{9})	—	2–9 (5.5_{2})	27–28 (27.5_{2})	11–26 (18.5_{2})	2–2 (2.0_{2})	3–19 (9.8_{21})	1–21 (10.8_{11})	0–1 (0.6_{8})	0–1 (0.7_{4})	1–2 (1.3_{6})	0 1 (0.1_{21})
28	—	—	0–3 (1.5_{9})	—	—	22–23 (22.5_{2})	10–27 (15.3_{4})	—	2–18 (9.0_{12})	12–28 (17.9_{8})	—	1–1 (1.0_{1})	1–3 (1.7_{6})	0–1 (0.5_{16})
29	—	—	0–5 (2.5_{2})	—	—	24 (24.0_{1})	5–32 (15.3_{1})	—	1–21 (9.4_{11})	8–29 (17.3_{9})	1–1 (1.0_{2})	1–1 (1.0_{2})	—	0–2 (0.8_{25})
30	—	—	5–9 (6.7_{4})	—	17–18 (17.5_{2})	16–30 (23.5_{4})	12–24 (17.4_{5})	—	5–11 (7.0_{3})	9–20 (14.8_{6})	—	2–2 (2.0_{2})	—	0–4 (0.7_{17})
31	—	—	0–13 (5.8_{11})	6–20 (13.0_{2})	14–23 (18.5_{2})	—	20–27 (24.0_{3})	—	8–22 (15.0_{2})	14–27 (17.8_{16})	1–4 (1.6_{10})	—	—	0–1 (0.3_{20})
32	—	—	1–14 (8.1_{7})	14–32 (22.2_{5})	—	—	15–24 (19.3_{3})	—	7–26 (14.0_{6})	11–44 (23.8_{11})	0–2 (1.1_{22})	—	—	0–5 (1.3_{12})
33	—	—	8–20 (13.3_{7})	7–43 (22.4_{8})	—	40–50 (44.5_{3})	20–33 (26.0_{5})	13–21 (16.7_{12})	30–46 (37.7_{3})	14–52 (29.0_{10})	1–5 (1.3_{20})	—	—	0–3 (1.3_{8})
34	—	—	1–34 (16.5_{8})	8–20 (14.1_{7})	—	19–57 (40.7_{9})	18–51 (35.8_{5})	20–21 (20.5_{2})	20–59 (36.6)	25–27 (25.6_{4})	1–4 (1.2)	—	—	0–4 (1.4_{4})
35	—	—	12–15 (13.5_{4})	7–58 (23.4_{8})	—	18–58 (43.0_{13})	26–67 (48.0_{3})	10–33 (21.4_{21})	39 (39.0_{1})	18–58 (36.2_{16})	1–7 (1.2_{33})	—	—	1–3 (2.3_{4})
36	—	—	13–34 (20.5_{6})	11–22 (18.6_{5})	—	58–61 (59.5_{2})	37–57 (47.8_{5})	14–44 (24.8_{17})	21–61 (39.0_{4})	24–46 (30.4_{7})	1–10 (2.5_{28})	—	—	5–10 (7.5_{2})
37	—	—	—	11–32 (18.0_{8})	—	27–49 (38.8_{6})	53 (53.0_{1})	10–53 (23.9_{17})	57 (57.0_{1})	20–53 (36.8_{5})	1–7 (1.9_{32})	—	1–1 (1.0_{2})	1–6 (3.5_{4})
38–42	—	15–19 (17.0_{2})	35–68 (47.9_{8})	20–73 (37.4_{23})	41–70 (55.2_{9})	30–55 (45.0_{5})	39–64 (49.4_{5})	19–61 (35.5_{30})	40–64 (49.5_{11})	26–59 (44.7_{17})	1–16 (2.7_{110})	8–20 (11.8_{6})	3–17 (10.7_{18})	1–8 (3.8_{8})
43–47	—	17–65 (44.2_{18})	14–75 (51.9_{16})	32–69 (56.8_{17})	41–69 (59.7_{4})	47–59 (53.5_{6})	29–62 (43.5_{4})	20–71 (44.2_{29})	35–62 (52.1_{17})	28–64 (49.7_{11})	0–26 (5.8_{18})	—	11–27 (16.6_{8})	—
48–52	—	50–69 (61.5_{11})	60–71 (65.8_{6})	42–68 (60.1_{12})	54–76 (68.0_{8})	—	58 (58.0_{1})	32–69 (49.9_{28})	49–63 (56.8_{6})	39–64 (46.6_{21})	1–15 (10.9_{5})	17–25 (21.3_{4})	11–27 (16.9_{10})	—
53–57	56–60 (58.0_{2})	46–75 (64.3_{8})	60–72 (66.3_{4})	42–68 (55.5_{4})	56–71 (64.3_{3})	—	—	51–65 (58.3_{6})	46–49 (47.5_{2})	26–61 (45.0_{4})	1–13 (4.7_{8})	15–20 (18.3_{4})	8–20 (14.4_{10})	—

(Table continued on next page.)

TABLE 12. CONTINUED.

Standard length (mm.)	*Rhinichthys osculus robustus* and modified populations										*R. o. reliquus*	*R. o. oligoporus*		*R. o. lethoporus*
	Carico L. Valley	Crescent Valley	Bishop Creek	Springs near Town Cr.	Ruby Valley	Potts Ranch	Dianas Punch Bowl	Coils Creek	Birch Ranch	Big Shipley Spring	Grass Valley	9.5 mi. S. of Wells	Warm Sprs., Clover Valley	Independence Valley
58–62	63–65 (64.0$_2$)	64–73 (67.7$_6$)	57–70 (64.3$_6$)	58–70 (64.0$_1$)	— —	— —	— —	32–65 (49.1$_8$)	— —	— —	1–28 (12.0$_{11}$)	— —	19–23 (21.0$_2$)	— —
63–67	56–68 (62.0$_2$)	66–83 (73.6$_{11}$)	— —	— —	— —	— —	— —	64–64 (64.0$_2$)	56–56 (56.0$_2$)	— —	3–30 (12.4$_{11}$)	— —	— —	— —
68–72	— —	67–80 (74.9$_{11}$)	— —	— —	— —	— —	— —	29–68 (43.6$_{10}$)	— —	— —	1–37 (18.8$_{12}$)	— —	— —	— —
73–77	— —	67–81 (76.0$_1$)	— —	— —	65–69 (67.0$_2$)	— —	— —	— —	— —	— —	2–22 (11.6$_{12}$)	— —	— —	— —
78–82	— —	62–81 (69.3$_6$)	— —	— —	— —	— —	— —	— —	— —	— —	7–20 (13.5$_2$)	— —	— —	— —
83–87	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
88–92	— —	77–79 (78.0$_2$)	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
Supratemporal canal:														
United	2	9	15	7	10	16	11	1	14	16	—	3	14	—
Interrupted	1	11	5	13	5	6	9	19	13	4	19	3	1	21

one side, was detected among 100 specimens that were checked on both sides. In neither race of *R. o. oligoporus* was any trace of a barbel found on either side, among 51 individuals. In *R. o. lethoporus*, among 75 specimens examined, we detected, on one side only, a minute barbel in three and a small barbel in one.

Rutter (1903, p. 148) described the barbels of *R. o. robustus* as "usually absent, present on 10 to 50 percent of specimens from any one locality." Snyder (1917, p. 67), who gave definite numbers, indicated a rather similar range for stream populations throughout the Humboldt system.[1] They may well have been dealing in part with local forms worthy of subspecific status, and may well have overlooked some rudimentary barbels.

Development Of The Lateral-line Pores

(See also p. 81; table 12; figures 25, 26.)

In most of the populations of *Rhinichthys osculus* here treated, the lateral-line pores on the body begin to form at a standard length of about 22 to 25 mm. They increase in number slowly at first, then increase rapidly at the length of about 25 mm., and begin to approach the final number at the length of about 35 to 40 mm. Relatively few specimens develop a full complement of pores, though completion is approached in a few populations. With age, the lateral line becomes well over half complete at the Locations listed above under *R. o. robustus*. The populations do differ somewhat in the rate of pore development (note, for example, the different rates illustrated on figure 26 for the dace from Potts Ranch and Coils Creek, from two Locations in the Monitor Valley branch of the Lake Diamond system). The fish from Crescent Valley develop an unusually large number of pores (fig. 25), probably because they attain an unusually large size and have many scales (table 18). But high scale number did not yield so many pores in the fish from Carico Lake Valley, and accompanied one of the lowest pore numbers in *R. o. reliquus*.

[1] See Supplementary Note (p. 253)

Lahontan Speckled Dace

Rhinichthys osculus robustus (Rutter).
(Figures 22 and 23.)

Pending the much needed and long deferred general review of the multitudinous local forms of the subgenus *Apocope* (defined above), we tentatively designate by this name the speckled dace of the Lahontan system and of certain basins that are part of that drainage complex, or almost certainly once were. In so doing, we follow Snyder (1917, pp. 67–69), who provisionally adopted the name *Agosia robusta* for the Lahontan representatives of "*Agosia*," although he recognized the high variability of speckled dace throughout the Lahontan system and questionably separated the Lahontan complex of forms from those in other major drainage systems. Snyder may have included separable subspecies (ordinarily, he did not recognize local forms within a stream basin, because of an obvious preconception that Western freshwater fishes are segregated, as full species, by major stream systems). Our decision to adopt the name *robustus* is based in part on the close agreement of our material from Carico Lake and Crescent valleys and from the headwater Bishop and Town creeks, and elsewhere in the Humboldt River system, with Rutter's type figure and description (1903, p. 148, 1 fig.) of *Agosia robusta*, from near the western rather than the eastern edge of the wide Lahontan system. Rutter's later reference (1908, pp. 139–140) to *Agosia robusta* of populations from various parts of the Sacramento River system is questionable, for more than one subspecies may well have been involved.

Points of agreement between our material from the Humboldt River system and Rutter's type description and figure include the rather faint and somewhat disrupted darkening of the primary dark lateral band and the weakness of the ventrolateral band; a definite though only moderately strong continuation onto the snout of the blackish lateral band; the rather extensive pigmentation of the lower sides; the usual lack or at most weak

development of horizontal dusky streaks along scale rows on side of trunk; the only moderately conspicuous blackening of the basicaudal black wedge; the blackening of the crotch of the rays to form a row of dashes near the middle of dorsal fin, and often, as a trace, in another row farther out on the fin; the only moderate speckling of the body; the frequent extension, though with interruptions, of the lateral line well toward the base of the caudal fin; the only moderate obliquity of the nearly straight mouth, with a rather thin and strongly blackened upper lip; the rather small size of the head; the similar, not depressed, form of the snout; the small size and rounded form of the fins; the insertion of the pelvic fin well before vertical from dorsal origin (on the average midway between base of caudal and a point just in advance of tip of snout); the rather robust form of the body anteriorly, becoming moderately attenuate behind; and the similarity in body proportions in general (table 13).

The Lahontan speckled dace has been treated as *Rhinichthys osculus robustus* by Hubbs and Miller (1948a, pp. 17, 19, 22–24, 28; 1948b, pp. 44, 102); Shapovalov and Dill (1950, p. 386); Shapovalov, Dill, and Cordone (1959, p. 172); and La Rivers (1962, pp. 21, 89, 430–432). The name was given as *Rhinichthys nubilus robustus* by La Rivers (1952, p. 99) and La Rivers and Trelease (1952, p. 117).

It is possible that an older name, based on material from some other stream system, may be found applicable to the common form of the Lahontan system. Certain of these extralimital forms seem separable (some perhaps even on the species level). Specimens from the Northwestern coastal area, which apparently should be called *R. o. nubilus* (Girard), have a much stronger dark lateral band (Schultz, 1936, p. 148). Collections from the upper and middle parts of the Colorado River system, representing *R. o. yarrowi* Jordan and Evermann and a chain of more or less sharply distinguishable forms from various tributaries, commonly to usually have a premaxillary frenum and otherwise look unlike *R. o. robustus*. In other drainage systems the frenum appears to be consistently lacking. In the Great Basin area under special treatment, for example, this was found to be true: most of the many specimens checked for presence or absence of the barbel, whether they came from the Humboldt River system or from the isolated basins, were simultaneously checked for presence or absence of a frenum, without finding any.

Rhinichthys o. robustus also seems to contrast with various populations that inhabit much of the area, largely in Utah, that during pluvial time drained into Lake Bonneville, immediately east of the area under detailed treatment. For example, a cursory examination shows that the Lahontan type, and its derivatives, differ sharply from the form inhabiting springs along West Deep Creek, 6 miles above Ibapah, in White Pine County, Nevada (near the midwestern margin of the Bonneville drainage, immediately east of our study area). Specimens from there (UMMZ 141410), probably representing *R. o. adobe* (Jordan and Evermann), differ from *R. o. robustus* in having a larger head; a lower, more nearly horizontal, and much larger mouth, with fuller lips, the upper of which is almost wholly devoid of pigment instead of being blackened; a larger and flatter snout; the lower sides barely marked by the second dark band, but generally darkened by horizontal dusky streaks along the scale rows (very seldom seen in the *R. o. robustus* series); a larger and more deeply blackened basicaudal wedge, and a much more definite black streak on the snout.

Rhinichthys o. robustus contrasts strongly with the forms herein described as distinct subspecies from basins adjacent to the Humboldt River system, and slight differences exist between the fish from the Humboldt headwaters and those comprising the remnant populations in the Lake Diamond system.

It seems to us highly probable that the populations of *Rhinichthys* inhabiting the isolated basins herein under special study were derived from *R. o. robustus* or an immediate ancestor. In this

view we hold some reservation in respect to the recently exterminated form of Grass Valley, which we somewhat hesitantly restrict to subspecies status, as *R. o. reliquus*: it may be a specifically distinct relict of ancient and somewhat uncertain origin.

Populations of Humboldt River System. (Figures 1, 12.)

Four populations in Nevada have been selected to represent as nearly as feasible the race(s) of *Rhinichthys osculus* that may be regarded as having originally occupied the basins of pluvial lakes Gilbert, Diamond, and Clover, wherein populations of this species are now rigidly restricted to very isolated springs, and wherein, especially in the Gilbert and Clover basins, the populations have become markedly differentiated. Two of these four populations are those of a spring in Carico Lake Valley and of Indian Creek in Crescent Valley, both of which are in lake valleys that during high flood discharge into Humboldt River. The other two populations are those of Bishop Creek and of springs adjacent to Town Creek, both near the town of Wells in eastern Nevada. These two latter Locations are in the perennial headwaters of Humboldt River, close to the divide that separates the Lahontan and Bonneville watersheds. These four Locations are designated R0 for the Carico Lake Valley spring and R1 for Indian Creek (fig. 1) and R2 and R3, respectively, for Bishop and Town creeks (fig. 12).

Location R0.—Unnamed warm spring in **Carico Lake Valley**, in the extreme-flood drainage of Humboldt River (*via* Crescent Valley); near the valley flat between Carico Lake (usually dry) and the foot of Big Sage Foothills of the Shoshone Range; shown on the U. S. G. S. Carico Lake quadrangle (1962) in the north-central part of Sec. 16 of T. 26 N., R. 45 E., near the center of Lander County, Nevada (fig. 1). Water clear; gravel and mud; *Nasturtium* very dense (had to be removed to catch specimens); 21° C. at 2 P.M. Patrick Coffin and D. Erickson, May 25, 1971; UMMZ 191774 (3 maturing females, 57–64 mm.); dip-net.

The dace were found only in the spring head, about 1 × 3 m. in area and 1 dm. deep. The outlet stream, which contained much less *Nasturtium* and was much shallower and only about 0.5 m. wide, with flow estimated at 0.25–0.5 cubic feet per second, flowed into and sank in a grassy pasture. The local conditions reemphasized the ability of speckled dace to maintain a population in a miniscule remnant habitat. A few other springs mapped in Carico Lake Valley may contain dace. Mr. Coffin reports that personnel of Nevada Department of Fish and Game know of no other fish in the valley, but that all the springs have not been examined. Hall and Iowa creeks, tributary to the south end of Carico Lake Valley, possibly have retained *Rhinichthys*, but almost surely not trout, as we have previously noted (Hubbs and Miller, 1948b, p. 36). However, the possibility of a former discharge into the Humboldt River system suggests need for further study. Mr. Coffin feels that recent droughts, including one ending about 1960, might have eliminated any fish in the streams. Presumably speckled dace are the only native fish in the Carico Lake basin. The hydrography of this basin has been treated by Everett and Rush (1966).

Location R1.—Indian Creek (also called Crums Creek), a western tributary to **Crescent Valley**, just above mouth of canyon near Tenabo, near boundary of T. 28–29, in western part of R. 47 E.; in mideastern Lander County, Nevada, about 5 miles above Dean Ranch, near center of valley, about 22 miles southwesterly from Beowawe (fig. 1). Clear water; sand, stones, mud, and trash; pools and riffles; little vegetation; 17° C. at mid-day (air 31°). Hubbs family and Miller, August 10, 1938 (M38-117); UMMZ 124908 (162, 13–88 mm.); 6-foot woven-mesh seine.

This was a small creek (about 0.6 to nearly 2.0 m. wide where fished); subject to floods. The dace here were large and common.

We heard at Dean Ranch, which is irrigated by the creek water, that the minnows come down pipes and ditches from about 5 miles above and cause trouble at the ranch. We noted that the dace were very wary, and tended to rush far downstream when disturbed—much more so than the spring-inhabiting dace (*R. o. reliquus*), just

previously observed in Grass Valley. Seemingly the behavior of this stock had been conditioned by their persistence in a canyon stream. The circumstance that this stream prior to ranch use had continued onto the valley floor probably led to the survival of the dace (in general, fishes have not survived in canyon streams in the Great Basin). On our 1938 expedition, we obtained the indication by brief exploration and by testimony at Dean Ranch that only dace live in Indian Creek and that this stream is the only fish-inhabited water in the entire valley. Our informer mentioned to us that a rancher who had long been in the valley had told him years previously that the minnows are native and that the waters of the great flood about four decades previously (about 1900) had filled not only the sump of Indian Creek just east of the ranch but also a series of dry lakes to the north, through which the water had overflowed on its course into the Humboldt River just above Beowawe, where houses had been washed away. The pluvial (and present flood-water) outlet course is detectable from the sump lake to Humboldt River not only by the chain of dry lakes, but also by banks and sand ridges. Since the great flood, the water had seldom reached even to the dry lakes on the ancient outlet course between the sump of Indian Creek and Humboldt River. We were told that this sump, locally called a "lake," ordinarily fills to a depth of a few inches each spring. It retained a little water in August, 1938. We were told that trout had been stocked in Indian Creek at about the time of the great flood, but that they did not survive.

Location R2.—**Bishop Creek**, near extreme headwaters of Humboldt River, above and below diversion dam, about 2 miles below Bishop Creek (Metropolis) Reservoir, and 2 miles above mouth of canyon, in T. 39 N., R. 62 E.; Elko County, Nevada, 9 miles (12 by road) almost due north of Wells (fig. 12). Rather muddy (at high stage; bottom visibility about 0.5 m.); very soft mud, sand, gravel, and boulders; generally very swift, locally very slight, current; some *Potamogeton*, cf. *P. pectinatus*, *Chara*, etc.; 21° C. above dam, 22° below (air 29°). Hubbs family, June 29, 1942 (H42-48); UMMZ 141522 (78, 18–60 mm.); 15-foot seine with ¼-inch square mesh.

The dace were not very common below the dam, and were rare above. Mature adults were taken on a gravel riffle. The stream here was partly fed by hot springs, which were said not to contain fish.

Location R3.—**Springs near Town Creek**, near main bend of stream, in northern part of T. 37 N., R. 62 E.; Elko County, 0.6 mile west of Wells, Nevada (fig. 12). Semi-stagnant; moderately firm peat to extremely soft organic mud, with some purple bacteria on bottom; virtually no current; marginal rushes, considerable *Chara*, and much floating vegetation; 22° C. (air 26°). Hubbs family, June 29, 1942 (H42–49); UMMZ 141524 (164, 15–59 mm.); 6-foot woven-mesh seine; many young discarded.

The dace were moderately common here. A local rancher reported that they had formerly been very abundant, that they had been used for bait, and that they had almost disappeared when the ponds had become nearly dry in the drought of 1934. "Swarms of little fish, none of them over four inches in length," were reported by Angel (1881, p. 18) to occur "in the valley near the town of Wells," "in apparently bottomless fountains of water miles from any surface streams" (see quotation on the flyleaf).

POPULATION IN RUBY VALLEY.

Location R4.—Isolated spring about 1 km. south of the southern boundary of the Ruby Lake National Wildlife Refuge in **Ruby Valley**, Nevada, in NW¼ Sec. 7, T. 25 N., R. 58 E.; White Pine County, 4.5 miles south of Elko County, Nevada (fig. 8). Donald E. Lewis, Refuge Manager, August 8, 1967 (Sample no. 2); UMMZ 186897 (32, 14–74 mm.).

Relictus was not included in the sample, but was obtained about 1 km. to the west.

During the course of locating extant populations of the relict dace, *Relictus solitarius*, in the Ruby Valley National Wildlife Refuge, Mr. Lewis surprised us by submitting, along with several series of that native fish, this small sample of *Rhinichthys osculus robustus*. After much thought, considerable correspondence, and a detailed study of the specimens, we came to the conclusion that the speckled dace had been intro-

duced into the valley, probably as escaped or dumped bait, and probably from the nearby headwaters of Humboldt River. The reasons for so thinking were as follows.

Until sport fishing was vigorously promoted in the Refuge, the relict dace was the only fish known from the enclosed basin of pluvial Lake Franklin, wherein the remnant waters in the area of Ruby Lake (pp. 198–199) were being restored for wildlife-refuge purposes.

In 1965 we found that the ponded waters of the Refuge were being very extensively fished for largemouth bass and other introduced sportfish, and that such utilization of the Refuge had been promoted by the issue and distribution of informational posters and leaflets. Ramps were provided for the convenience of anglers. The Nevada Fish and Game Department was operating a fish hatchery within the limits of the Refuge (where regulated public shooting was also being promoted). Because of the remote location, much of the angling was by residents of the general area. Many of the fishermen came from Wells, the nearest town. Fishermen from there and from other towns on the Humboldt River would have had easy access to speckled dace for use as bait. As is mentioned above, the minnows (speckled dace) of Town Creek, close to Wells, had been used for bait. Anglers from the only other towns within a reasonable distance, principally Ely, would not have had ready access to *Rhinichthys*.

The detailed tabulations of characters of the various populations of *Rhinichthys osculus* (tables 11–18) demonstrate in general very close agreement between the sample from the Location R4 in Ruby Valley and those from the Humboldt River headwaters, particularly Town Creek. The agreement is complete in the distinctive features, noted above (pp. 104–105), of *Rhinichthys osculus robustus*. Agreement is excellent in fin-ray numbers (table 15). Vertebrae (table 16) average somewhat higher than expected, perhaps because of the direct action of the environment, or because the limited stock of introduced fish happened to carry genes for the higher average. Agreement is excellent in lateral-line pore development (table 12; fig. 25), but the barbel development (table 11) averages slightly greater than expected, perhaps for such a reason as suggested for the vertebrae. Agreement is adequate in other respects.

It was suspected that the minnows might have been stocked for forage or have been distributed accidentally long with bass or other gamefish, much as *Lucania parva* (Baird and Girard) was established in Utah and southern California (Hubbs and Miller, 1965, pp. 48–49), but the Refuge Manager at first assured us that this had not been done and would have been contrary to Refuge policy. (On our urging, the late J. Clark Salyer, then head of the federal refuge system, issued implicit instructions to prohibit introductions.) Later, however, Mr. Lewis obtained from the records of the Nevada State Fish and Game Department the following account of an earlier stocking:

> September 8, 1950: Dace [presumably *Rhinichthys osculus robustus*] and red-striped shiner [obviously *Richardsonius egregius*] (No. 3000) were placed in the South Sump area (Water gape [?], County Line Pond and Willow Pond). Source of fish—Tea Creek.
>
> Tea Creek location and drainage: Tea Creek originates in the Jarbridge Mountains, 30 miles north of Deeth, Nevada. Tea Creek flows into the Mary's River, then into the Humboldt River.

This statement obviously refers to the introduction of minnows as forage into the general region wherein *Rhinichthys* was collected.

After this discussion of the introduction of the speckled dace into Ruby Valley from a Humboldt River headwater was written, it was noted that La Rivers (1962, p. 432) had reported an introduction of *Rhinichthys osculus robustus* into Ruby Valley, as follows:

> Like all the small "minnows," speckle dace have been widely used as bait fish and as such have been carried about by fishermen. To what extent this has occurred is indeterminable, but one instance of official planting of

> this type is known. In August of 1951, the Nevada Fish and Game Commission obtained some specimens from Sadler's Ranch in Diamond Valley, Eureka County, and planted them in Ruby Marsh, Elko County, as forage fish for the Largemouth Blackbass fishery there.
>
> Prior to this, the marsh suffered from lack of forage fishes, this lack being supplied by smaller blackbass, to the general detriment of the fishery. The speckle dace seem to be well established in the Marsh, but apparently in sections more-or-less inaccessible to blackbass.

In view of our findings in 1934, the "speckle dace" said to have become well established after this stocking were native relict dace, rather than offspring of *Rhinichthys osculus robustus* brought in from the Sadler Ranch, and it seems probable that the stock from there did not survive. Comparison of specimens in 1971 showed that the series from Bishop Creek in the Humboldt system (UMMZ 141522) agreed closely with those from Ruby Valley (UMMZ 186897) and contrasted with the large collection from Big Shipley Spring (at Sadler Ranch) in general appearance, including the strength of the basicaudal spot; in the less posteriorly inserted dorsal fin (distance from dorsal insertion to caudal base when stepped forward extending in males to some point between front of orbit and front part of snout, rather than, usually, to some point within or just behind eye, and extending in females usually to some point within eye, rather than from rear edge of eye to well behind eye); in the less complete lateral line; and, in general, in the slenderer caudal peduncle.

It will be interesting to determine whether this dace will multiply and spread through Ruby Valley. It apparently would not be prevented by the preoccupation of the area by the native relict dace, for that species has been so nearly wiped out in the valley that it persists only in isolated springs to which bass have not gained access (pp. 197–199). Very likely this predator will also block the establishment of speckled dace. We found no evidence that *Richardsonius* had gained a foothold in the valley.

The persistence in the spring in Ruby Valley of the characters of *R. o. robustus* has a bearing on the genetic integrity of the differentiated populations of other isolated desert springs—constituting, in effect, a natural experiment (see p. 80).

Characters of Populations of *Rhinichthys osculus robustus* Sampled from the Humboldt River System.

Analysis of the characters of these populations has shown considerable heterogeneity, though within a single general pattern. We briefly treat the local variation shown by the samples from Carico Lake Valley and Crescent Valley, Bishop Creek, and springs near Town Creek; and for the stock in Ruby Valley assumed to have originated by introduction from a Humboldt River headwater.

Size. The dace of Crescent Valley are among the largest of the species, definitely larger than those of other Humboldt samples studied (table 20), which are of average size. They exceed in size all other populations of *Rhinichthys* treated in this report. The large females are roughly matched by the larger females of *R. o. reliquus*, but the adult males in Crescent Valley are markedly larger than the largest taken in Grass Valley.

Coloration. These series, typical of *R. o. robustus* (p. 104), are relatively uniform in color pattern and in life color.

Form. In form of body and head these lots are also typical of *R. o. robustus*.

Barbel. In four of the five series the barbel is more often developed than absent, and is as often present as absent in the 3 fish from Carico Lake Valley. The barbel in all series is more frequently judged 'absent' or 'small' rather than 'large' (table 11).

Lateral line. The development of the lateral line, in terms of the number of pores, progresses at a relatively similar rate in all Humboldt samples (table 12, fig. 25), much as in the races from Diamond Valley, but much more rapidly, and

TABLE 13. *Proportional measurements, in permillage of standard length, for representative series of adults of populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Sex / Subspecies / Pluvial lake system / Locality	No.	S.L., mm.	Predorsal	Anal to caudal	Body depth	Peduncle depth	Head length
MALES							
R. o. robustus							
L. Lahontan (Humboldt R.)							
Crescent Valley	10	43–64(52)	533–564(553)	356–385(368)	230–261(245)	114–134(127)	246–268(254)
Bishop Creek	8	37–45(42)	512–565(544)	325–376(353)	221–270(240)	113–136(122)	251–302(269)
Springs near Town Cr.	20	31–47(38)	548–589(569)	305–372(347)	220–268(246)	107–135(119)	261–293(279)
L. Franklin (introduced)							
Ruby Valley	4	40–41(41)	541–558(547)	341–366(354)	237–259(251)	131–146(139)	284–285(284)
L. Diamond							
Potts Ranch	10	34–37(35)	570–613(589)	327–361(345)	248–301(277)	126–158(143)	272–299(284)
Dianas Punch Bowl	10	30–38(34)	548–592(577)	317–356(337)	221–252(237)	122–136(129)	271–301(288)
Coils Creek	20	32–49(42)	542–600(573)	308–368(347)	233–267(249)	119–147(133)	259–299(284)
Birch Ranch	15	33–41(37)	540–586(566)	313–367(349)	225–268(251)	123–155(140)	264–289(271)
Big Shipley Spr.	15	31–37(34)	558–623(591)	303–354(330)	247–283(263)	127–154(136)	276–304(289)
R. o. reliquus							
L. Gilbert							
Grass Valley	20	34–47(40)	572–618(592)	292–357(316)	223–265(236)	125–148(135)	252–296(273)
R. o. oligoporus							
L. Clover							
9.5 mi. S. of Wells	3	40–41(40)	573–591(581)	359–364(361)	219–277(248)	125–143(133)	270–273(271)
Warm Sprs., Clover V.	12	28–44(39)	540–598(566)	331–375(361)	215–284(243)	120–142(134)	247–280(262)
R. o. lethoporus							
L. Clover							
Independence Valley	12	28–34(30)	552–609(583)	302–367(337)	244–305(276)	135–159(148)	272–300(285)
FEMALES							
R. o. robustus							
L. Lahontan (Humboldt R.)							
Crescent Valley	10	45–88(64)	548–591(566)	342–380(358)	244–278(259)	114–137(123)	240–261(249)
Bishop Creek	11	45–60(52)	539–591(563)	338–375(353)	239–300(265)	107–125(116)	253–284(265)
Springs near Town Cr.	20	30–59(43)	562–610(583)	324–356(339)	234–287(256)	109–137(120)	267–293(280)
L. Franklin (introduced)							
Ruby Valley	7	45–74(53)	548–578(566)	324–356(337)	234–270(246)	119–149(130)	269–298(280)
L. Diamond							
Potts Ranch	10	30–46(38)	577–615(599)	321–355(333)	251–296(274)	118–145(135)	276–313(287)
Dianas Punch Bowl	10	34–47(39)	553–599(587)	286–341(317)	227–266(245)	114–136(125)	274–316(293)
Coils Creek	20	37–71(54)	541–618(580)	318–367(340)	237–302(265)	123–144(131)	266–317(284)
Birch Ranch	20	36–65(46)	565–599(583)	321–355(333)	236–293(271)	114–142(134)	251–302(268)
Big Shipley Spr.	21	36–55(47)	571–607(590)	305–347(321)	226–279(254)	114–139(125)	258–292(279)
R. o. reliquus							
L. Gilbert							
Grass Valley	20	35–82(60)	560–603(585)	281–331(301)	226–274(245)	115–141(127)	252–291(273)
R. o. oligoporus							
L. Clover							
9.5 mi. S. of Wells	4	51–55(53)	555–587(577)	317–363(338)	259–293(270)	129–136(132)	265–273(269)
Warm Sprs., Clover V.	15	28–59(50)	564–612(584)	320–354(336)	224–272(250)	115–133(127)	233–275(258)
R. o. lethoporus							
L. Clover							
Independence Valley	12	32–39(36)	569–614(584)	320–355(334)	257–305(278)	137–162(145)	276–327(287)

[1] For each character there is stated the minimum and maximum values and, in parentheses, the mean value. When available, a graded series of sizes was selected from among the better preserved specimens. In some series, occasional measurements had to be omitted, particularly for the caudal-fin length.

(Table continued on next page.)

TABLE 13. CONTINUED.

Sex / Subspecies / Pluvial lake system / Locality	No.	S.L., mm.	Head depth	Head width	Snout length	Orbit length	Upper jaw	Inter-orbital
MALES								
R. o. robustus								
L. Lahontan (Humboldt R.)								
Crescent Valley	10	43–64(52)	148–169(161)	137–159(144)	79–91(84)	46–54(50)	69–75(72)	76–89(83)
Bishop Creek	8	37–45(42)	163–185(171)	135–162(146)	83–96(90)	56–63(60)	67–79(73)	82–100(91)
Springs near Town Cr.	20	31–47(38)	159–197(180)	129–164(146)	83–94(88)	55–73(62)	62–84(78)	71–98(87)
L. Franklin (introduced)								
Ruby Valley	4	40–41(41)	189–194(192)	154–170(163)	80–94(87)	55–58(56)	78–92(85)	91–92(91)
L. Diamond								
Potts Ranch	10	34–37(35)	189–205(198)	150–175(160)	80–96(88)	62–68(65)	64–81(75)	94–100(98)
Dianas Punch Bowl	10	30–38(34)	183–206(192)	150–178(160)	80–95(89)	58–76(66)	77–89(83)	90–113(99)
Coils Creek	20	32–49(42)	181–205(192)	147–179(158)	83–97(90)	52–74(61)	75–93(82)	77–107(93)
Birch Ranch	15	33–41(37)	174–196(186)	138–162(149)	80–91(86)	57–72(65)	70–90(80)	85–103(93)
Big Shipley Spr.	15	31–37(34)	185–218(198)	145–172(155)	82–99(88)	65–77(72)	76–93(86)	84–104(95)
R. o. reliquus								
L. Gilbert								
Grass Valley	20	34–47(40)	176–201(186)	128–160(146)	78–94(84)	54–67(61)	74–89(83)	76–97(87)
R. o. oligoporus								
L. Clover								
9.5 mi. S. of Wells	3	40–41(40)	186–191(189)	142–161(153)	80–89(85)	63–66(65)	69–76(72)	89–96(92)
Warm Sprs., Clover V.	12	28–44(39)	172–199(188)	145–169(157)	78–93(86)	51–70(59)	66–80(73)	80–101(90)
R. o. lethoporus								
L. Clover								
Independence Valley	12	28–34(30)	188–207(195)	147–172(156)	78–87(82)	64–75(70)	73–88(79)	90–104(97)
FEMALES								
R. o. robustus								
L. Lahontan (Humboldt R.)								
Crescent Valley	10	45–88(64)	157–171(165)	141–159(149)	83–93(86)	42–56(47)	71–81(76)	78–90(86)
Bishop Creek	11	45–60(52)	158–185(169)	134–163(149)	80–98(89)	47–67(56)	63–82(74)	83–97(91)
Springs near Town Cr.	20	30–59(43)	172–192(181)	141–166(153)	83–102(92)	50–74(60)	69–89(81)	87–108(94)
L. Franklin (introduced)								
Ruby Valley	7	45–74(53)	173–193(185)	155–193(165)	87–101(93)	47–56(52)	75–87(82)	88–105(98)
L. Diamond								
Potts Ranch	10	30–46(38)	184–205(195)	148–185(163)	84–99(92)	56–76(65)	68–92(82)	92–106(97)
Dianas Punch Bowl	10	34–47(39)	181–206(193)	150–170(162)	88–98(94)	53–70(60)	84–92(89)	98–106(102)
Coils Creek	20	37–71(54)	179–200(189)	155–193(171)	86–103(93)	44–67(54)	70–91(82)	90–105(97)
Birch Ranch	20	36–65(46)	172–205(185)	137–172(157)	85–101(90)	51–68(59)	74–100(81)	86–106(94)
Big Shipley Spr.	21	36–55(47)	176–198(187)	142–164(155)	81–98(90)	52–69(61)	78–98(86)	86–108(97)
R. o. reliquus								
L. Gilbert								
Grass Valley	20	35–82(60)	171–200(184)	141–171(153)	81–98(89)	44–63(51)	72–89(83)	77–92(86)
R. o. oligoporus								
L. Clover								
9.5 mi. S. of Wells	4	51–55(53)	203–207(205)	167–181(175)	85–94(90)	57–62(60)	73–79(77)	95–102(99)
Warm Sprs., Clover V.	15	28–59(50)	176–198(186)	142–176(156)	80–95(89)	48–69(54)	69–93(78)	85–100(93)
R. o. lethoporus								
L. Clover								
Independence Valley	12	32–39(36)	184–207(196)	142–178(162)	77–95(85)	63–77(69)	75–87(80)	90–110(97)

(Table continued on next page)

TABLE 13. CONTINUED.

Sex / Subspecies / Pluvial lake system / Locality	No.	S.L., mm.	Sub-orbital	Depressed D.	Caudal length	Pectoral length	Pelvic length
MALES							
R. o. robustus							
L. Lahontan (Humboldt R.)							
Crescent Valley	10	43–64(52)	43–50(47)	194–240(209)	218–255(241)	216–244(230)	161–182(171)
Bishop Creek	8	37–45(42)	40–56(46)	224–245(235)	249–274(262)	229–259(243)	161–197(179)
Springs near Town Cr.	20	31–47(38)	39–54(45)	202–237(224)	220–285(253)	216–272(242)	150–197(171)
L. Franklin (introduced)							
Ruby Valley	4	40–41(41)	44–49(47)	205–243(221)	249–279(258)	237–258(245)	164–179(172)
L. Diamond							
Potts Ranch	10	34–37(35)	44–58(49)	206–232(216)	226–261(240)	225–242(234)	147–164(159)
Dianas Punch Bowl	10	30–38(34)	43–59(49)	199–239(224)	233–275(259)	231–288(251)	153–181(167)
Coils Creek	20	32–49(42)	42–52(46)	206–248(223)	222–280(249)	245–280(260)	161–202(181)
Birch Ranch	15	33–41(37)	43–52(47)	211–239(223)	236–270(255)	204–261(240)	146–185(168)
Big Shipley Spr.	15	31–37(34)	39–57(47)	208–243(224)	246–292(259)	226–283(255)	143–177(161)
R. o. reliquus							
L. Gilbert							
Grass Valley	20	34–47(40)	41–52(46)	196–237(219)	228–274(251)	229–269(249)	134–172(155)
R. o. oligoporus							
L. Clover							
9.5 mi. S. of Wells	3	40–41(40)	40–46(42)	223–258(235)	264–287(276)	221–236(229)	150–183(167)
Warm Sprs., Clover V.	12	28–44(39)	37–46(42)	213–242(230)	244–287(262)	198–242(219)	153–171(164)
R. o. lethoporus							
L. Clover							
Independence Valley	12	28–34(30)	34–43(39)	208–248(227)	246–270(256)	217–252(232)	134–168(152)
FEMALES							
R. o. robustus							
L. Lahontan (Humboldt R.)							
Crescent Valley	10	45–88(64)	44–54(47)	185–222(201)	205–251(226)	179–203(191)	140–161(151)
Bishop Creek	11	45–60(52)	43–51(47)	196–225(211)	236–267(248)	188–215(197)	137–164(154)
Springs near Town Cr.	20	30–59(43)	42–56(49)	199–242(216)	232–259(243)	178–216(199)	143–169(155)
L. Franklin (introduced)							
Ruby Valley	7	45–74(53)	46–53(49)	201–230(214)	225–253(244)	180–210(197)	140–159(146)
L. Diamond							
Potts Ranch	10	30–46(38)	43–53(50)	207–222(216)	251 (1 ex.)	182–215(196)	139–157(150)
Dianas Punch Bowl	10	34–47(39)	46–56(52)	188–220(203)	233–266(247)	186–209(196)	137–161(146)
Coils Creek	20	37–71(54)	45–57(50)	188–229(209)	204–276(239)	189–224(208)	145–183(162)
Birch Ranch	20	36–65(46)	43–55(48)	193–240(207)	207–263(235)	174–223(196)	134–163(146)
Big Shipley Spr.	21	36–55(47)	42–54(48)	193–217(202)	224–263(240)	178–214(198)	130–164(149)
R. o. reliquus							
L. Gilbert							
Grass Valley	20	35–82(60)	42–55(49)	169–221(198)	207–268(232)	166–205(182)	126–160(139)
R. o. oligoporus							
L. Clover							
9.5 mi. S. of Wells	4	51–55(53)	41–49(45)	195–218(207)	224 (1 ex.)	165–186(176)	132–155(141)
Warm Sprs., Clover V.	15	28–59(50)	39–48(44)	186–225(204)	212–268(241)	163–190(176)	120–154(136)
R. o. lethoporus							
L. Clover							
Independence Valley	12	32–39(36)	38–54(43)	190–232(209)	215–268(249)	168–193(180)	132–159(143)

much farther, than in the other subspecies here treated (figs. 25, 26). The Crescent Valley sample, of outstandingly large fish, shows a less rapid increase at first, but eventually continues to a somewhat higher level. A similar relation holds for the Coils Creek sample in the Lake Diamond series (p. 104).

SUPRATEMPORAL CANAL. This canal is somewhat variably either united or interrupted in these five samples (table 12).

MORPHOMETRY. There are some deviations among the four main samples in morphometric proportions (table 13). The dorsal and anal fins tend to be more posterior than usual in springs near Town Creek. The body and the caudal peduncle tend to be deepest in the Ruby Valley sample. There is some fluctuation, rather inconsistent, in length of the head and of the head parts, but the fin measurements are rather uniform.

SEXUAL DIMORPHISM AND NUPTIAL CHARACTERS. The degree of sexual difference in predorsal length and in the size of the fins is about average and is relatively uniform among the four main samples (table 14). On the average, the difference in the size of the dorsal fin is greatest in the Bishop Creek sample.

FIN RAYS. There is little variation among the four main samples in number of fin rays (table 15). For the pelvic count there is a weak cline, decreasing eastward.

VERTEBRAE. There is also some fluctuation in counts of precaudal, caudal, and total vertebrae (table 16). The averages are lowest for Bishop Creek and highest for the three specimens from Carico Lake Valley; the caudal and total counts are highest for Ruby Valley (see also p. 108). The samples from Crescent Valley and Bishop Creek seem slightly but significantly different. In the samples from Carico Lake and Crescent valleys the position of the pelvic-fin insertion (table 17) is farther back on the average, in reference to the overlying vertebrae, than in the Humboldt headwater series.

SCALE ROWS. In correlation with the vertebral counts the scale-row counts (table 18) are on the high side for the samples from Carico Lake and Crescent valleys and on the low side for Bishop Creek.

GILL-RAKERS. The raker counts are relatively uniform.

SEXUAL DIFFERENCES IN NUMBERS AND BIOMASS. Not striking (table 19).

The moderate inter-sample variation within the Humboldt River system series is also referred to in the following account of the populations in the Lake Diamond system.

POPULATIONS OF THE PLUVIAL LAKE DIAMOND SYSTEM.

Field exploration and frequent local inquiry have disclosed only five isolated spring populations of *Rhinichthys osculus* in the extensive drainage system of pluvial Lake Diamond, Nevada (pp. 17–20). We think that some additional stocks may inhabit springs along an apparent fault line close to the western edge of the playa of the ancient sump lake, particularly in the general vicinity of Big Shipley Spring (p. 17). The occurrence in Roberts Creek of fish that may be speckled dace has been hinted (p. 19). There is no evidence that other isolated stocks occur in the drainage system. The evidence is further discussed following the accounts of the several Locations.

Location R5.—Hot-spring outflow on **Potts Ranch** (previously known as Wilson Ranch), issuing at the south end of a lava hill immediately east of Stoneberger Creek, a largely intermittent stream, in the Monitor Valley division of the Diamond Valley drainage system, near the boundary line of Sec. 1–2, T. 14 N., R. 47 E.; Nye County, Nevada (fig. 3). Clear water; rather firm clay and muck; generally swift; *Potamogeton*, cf. *P. pectinatus*, over about one-fourth of bottom; 32–34° C. where fished (hotter above—fig. 20; air 24°). Hubbs family, August 16, 1938 (M38-132); UMMZ 124937 (103, 19–46 mm.); 6-foot woven-mesh seine.

Whether *Rhinichthys* still persists in the outflow of the hot spring on Potts Ranch is unknown to us. An examination of the spring area (fig. 20, based on a rough field sketch of August 16, 1938) suggested that prior to the extensive ditch-

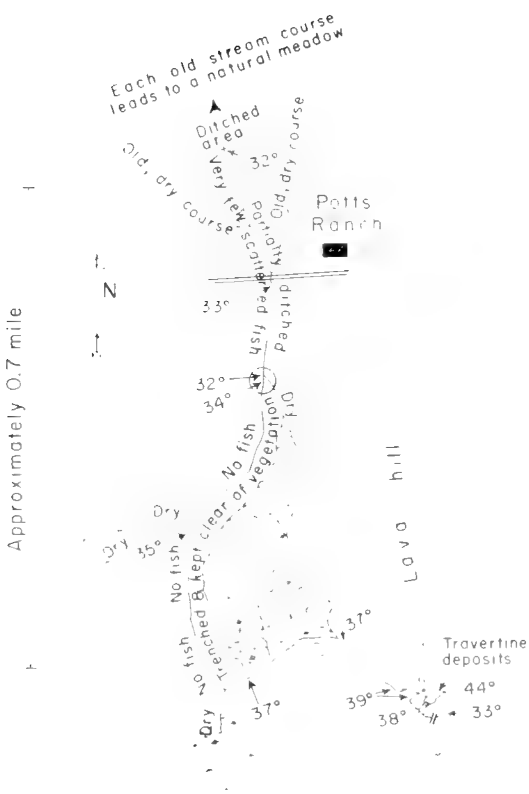


FIGURE 20. Map of warm springs on Potts Ranch, Monitor Valley, Nye County, Nevada (Location R5), sketched, with temperature records added, when fish collection M38-122 was made on August 16, 1938: three-fourths of the fish were taken in the encircled area.

ing of the outflow into hay meadows the dace probably abounded in the cooling stream courses that had previously existed, south of the ranch house, in the natural meadow west of the lava hill, just as in 1938 they still persisted in the then still natural outflow of Big Shipley Spring (Location R8). Three-fourths of the dace were collected where seepage from the former meadow area below the springs rose in the old channel just before it received the trenched ditch that bypassed the old meadow (this small area of chief collecting is circled on the map; here temperatures were recorded as 32° and 34° C.). No fish were taken above this area, in the trenched ditch kept clean of vegetation, and the only dace seen, at a point in the ditch where 37° was recorded, was swimming erratically against the bank, in *Chara*. None were seen near the spring sources, in water at 38–44° C. Below the very limited area where most of the population was concentrated, in the kilometer above the dispersal of the flow in ditches, the dace were very few and scattered. It seemed quite obvious that the handling of the water had endangered the isolated, remnant fish population. It was evident that the supply had been decimated to the point where Mr. Potts was unsure that any had survived. A few years earlier they had been, he reported, very numerous.

Location R5A.—Hot-spring outflow around **Dianas Punch Bowl**, at source of short flow of south fork of Stoneberger Creek in Monitor Valley division of the Diamond Valley drainage system, near center of south border of Sec. 22, T. 14 N., R. 47 E.; Nye County, Nevada (fig. 3). Three samples.—(1) Labeled as Dianas Punch Bowl outflow, about 100 m. upstream from travertine barrier to surface flow; 37.5° C.; Robert E. Brown, February 9, 1972 (99, 21–48 mm.).[3] (2) Labeled as outflow from Dianas Punch Bowl, about 200 m. downstream from barrier to surface flow; 37° C.; dissolved oxygen 2.0 ± 0.2 mg./l.; Robert E. Brown, February 9, 1972 (54, 22–43 mm.).[3] (3) Labeled as outflow of Dianas Punch Bowl, but as from about 300 m. downstream from the most western major spring; 39.0° C. (by calibrated thermister recorder); dissolved oxygen 1.8 ± 0.2 mg./l. (Hach dissolved-oxygen kit); Robert E. Brown and Thomas M. Jenkins, Jr., February 19, 1972 (40, 30–47 mm.).[3] These spring waters are further discussed on p. 20.

Location R6.—Spring-fed pool (about 5 × 7 m.) in grass meadow along the essentially dry **Coils Creek**, at Three Bar Ranch, 43.5 miles by Roberts Creek Road northwest of Eureka (Coils Creek arises between the Toiyabe Range and the Red Hills section of Roberts Mountains, and flows, in flood, through Kobeh Valley and Bean Flat to join the flood drainages of Monitor and Antelope valleys, thence to pass through Devils Gate to enter the dry lake bed of Diamond Valley); located near boundary line T. 22–23 N., at about middle of R. 49 E.; near west edge of Eureka County, Nevada (fig. 3). Moderately clear water; rather firm clay and mud; no current; rushes, *Equisetum*, and *Potamogeton*,

[3] The specimens so listed are those utilized in this paper; some were returned to the collector, who has taken other examples in January and in June, 1972.

cf. *P. pectinatus*; 14° C. (air 21°); Hubbs family and Miller, August 15, 1938 (M38–127); UMMZ 124935-36 (1,136, 13–17 mm.); derris.

Except for a report of fish thought not to be trout, which might have been speckled dace, in a small valley in the course of Roberts Creek (p. 19), no indication was obtained of native fish life in any other waters in the northern part of the western arm of the flood-water drainage basin (p. 20).

Location R7 (and G5).—Two large springs on **Birch Ranch** (Jorge Jacobsen's at time of collecting; "Thompson Ranch" on Ely 1:250,000 map), on east side of Diamond Valley near south end of Alkali Desert, at west base of Diamond Mountains, near north margin of T. 23 N., R. 54 E.; close to east boundary of Eureka County, Nevada (figs. 3, 8). Water (in ditch 2–3 m. wide and in pond) clear and somewhat sulphurous; fairly firm clay and mud; moderate to slight current; considerable growth of rushes, *Naias marina*, *Utricularia*, etc.; 22° C. at 7:30 A.M. (air 13°). Hubbs family and Miller, August 13, 1938 (M38–126); UMMZ 124932 (188, 17–65 mm.); 6-foot woven-mesh seine and 25-foot seine with 1/4-inch square-mesh in bag.

Mr. Jacobsen, who had been at the Birch Ranch for 35 years, believed that the dace and the chub (the modified local form of *Gila bicolor obesa* discussed on pp. 18, 154) were native, and that they were the only fish on the east side of Diamond Valley. We found the two species living here together, in both ditch and pond, without any evident hybridization. No indication was obtained that any native fish had survived elsewhere on the east side of Diamond Valley (p. 154).

Location R8.—Outflow from a small lake (fig. 21 and Eakin, 1962, inside front cover), the impoundment of **Big Shipley Spring** (recently mapped as Shipley Hot Spring), at the Sadler Ranch, south of the ranch houses, near middle of west side of Alkali Flat, at the foot of Sulphur Springs Range, in T. 14 N., R. 52 E.; in mid-eastern Eureka County, Nevada (figs. 3, 8). Water clear, slightly sulphurous; mud, sand, and hot-spring deposits; moderate to slight current; considerable rushes, *Naias marina*, *Utricularia*, etc.; 28° C. at 7:30 A.M. (air 19°). Hubbs family and Miller, August 13, 1938 (M38–123); UMMZ 124930–31 (415, 22–55 mm.); 6-foot woven-mesh seine and 15-foot seine with 1/4-inch square mesh. The bottom of the pond away from the large springs, which issued at 102° F. (39° C.), at the main source, was covered with *Utricularia* and *Naias marina*.

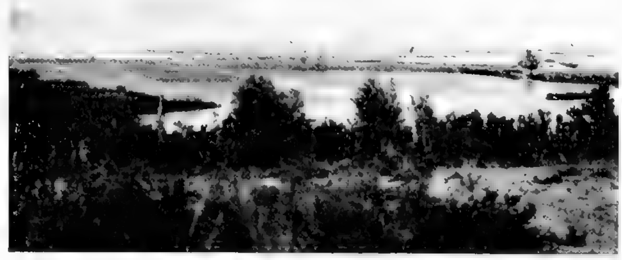
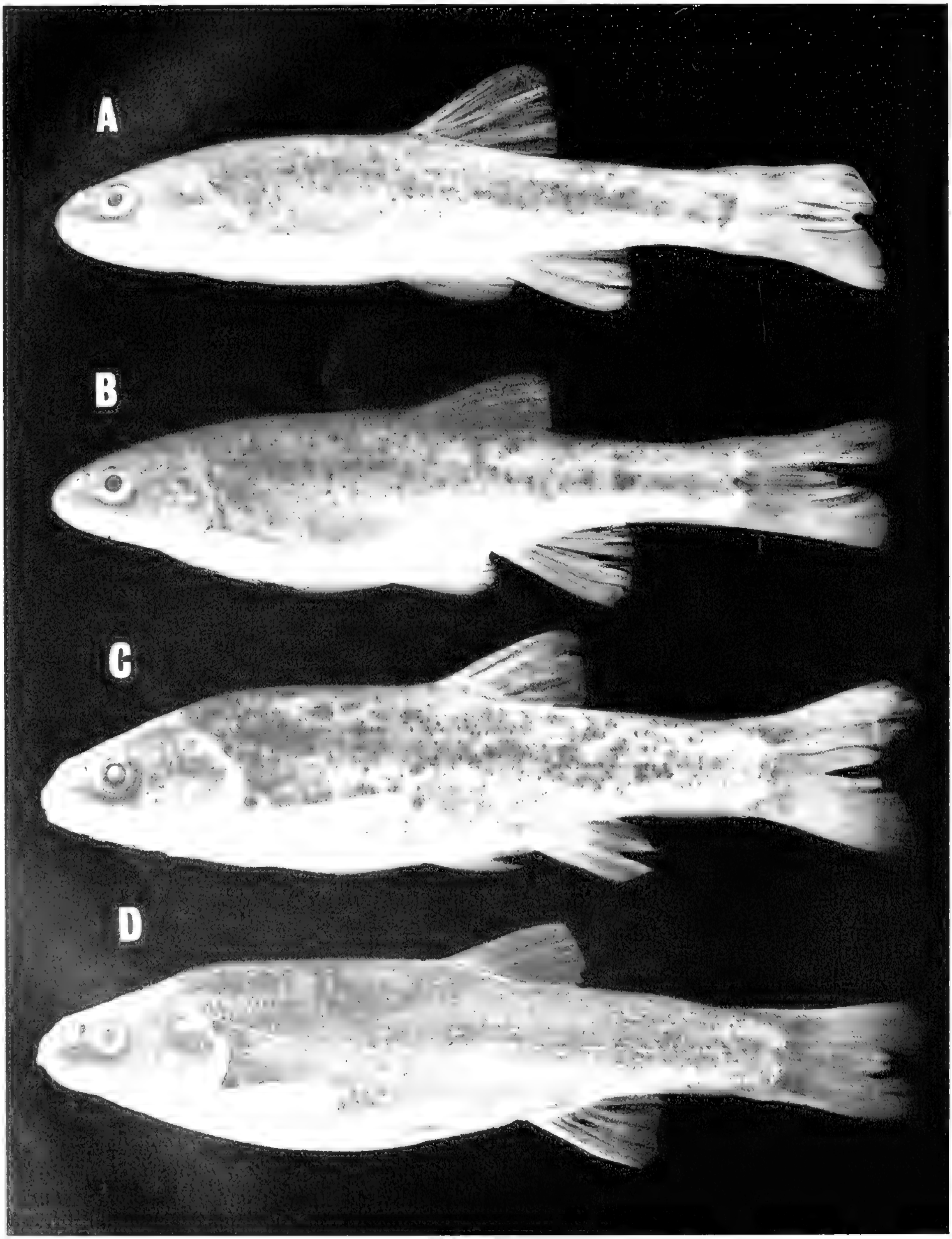


FIGURE 21. Ponded head of Big Shipley Spring, at Sadler Ranch, Diamond Valley, Eureka County, Nevada, overlooking Alkali Flat (the bed of pluvial Lake Diamond). Outlet of pond (Location R8) yielded a race of *Rhinichthys osculus robustus*. Photographed by Laura C. Hubbs, August 12, 1938.

The dace were found in abundance (and were seen nowhere else) in the large outflow stream below a natural falls about 2 m. high, especially in channels among the rushes. Above the falls, and in the large ditch leading toward the ranch houses, only goldfish, *Carassius auratus* (Linnaeus), were taken, and only this exotic was seen in the pond and in ditches close by; and the goldfish were in all the ditches. The goldfish had been planted by the rancher (Mr. Sadler).

Characters of Populations Referred to *Rhinichthys osculus robustus*, in the Lake Diamond Drainage System.

Characteristics of the speckled dace from each of the five Locations, just described, within the large pluvial Lake Diamond drainage basin, are different in small ways from one another and from those of *Rhinichthys osculus robustus* of the Humboldt River system. The differences, however, in our judgment, are hardly trenchant enough to warrant subspecific separation. The differences


A
B
C
D

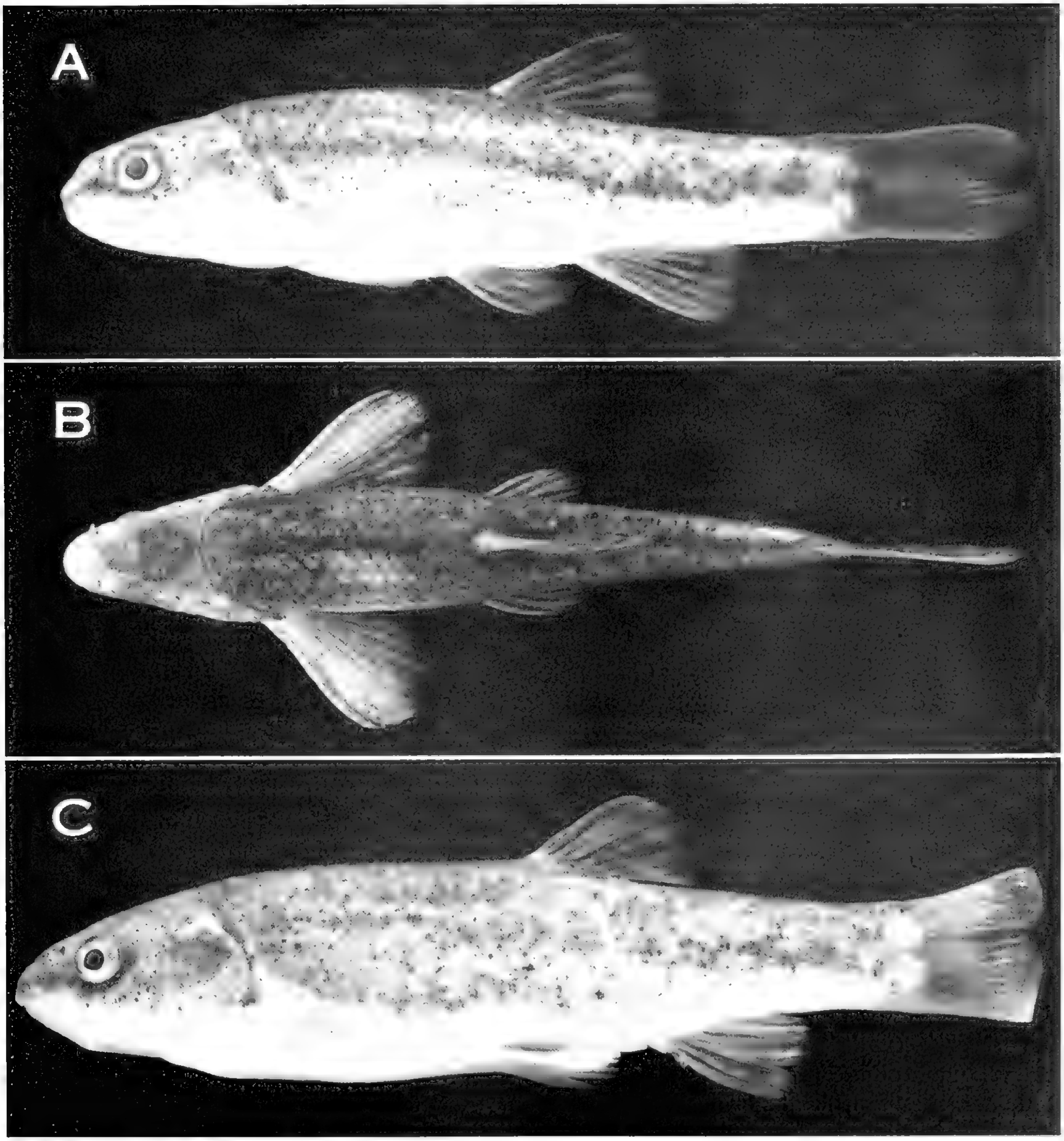


FIGURE 23. *Rhinichthys osculus robustus*, races from Diamond Valley, Nevada. A. Birch Creek (Location R7): UMMZ 124932, no. 21; male, 40.2 mm., side view. B. Same specimen, top view, showing nuptial tubercles and form of pectoral fin. C. Big Shipley Spring (R8): UMMZ 124930, unnumbered specimen; female, 53.3 mm

←

FIGURE 22. *Rhinichthys osculus robustus*, from drainage basins of Humboldt River and pluvial Lake Diamond Nevada. A. Bishop Creek (Location R2): UMMZ 141522, no. 14; male, 44.7 mm. B. Same catalog number, no. 8; female, 45.1 mm. C. Coils Creek (R6): UMMZ 124936, no. 29; male, 43.5 mm. D. Same field collection: UMMZ 124935, no. 2; female, 71 mm.

certainly are less impressive than are those that distinguish from one another and from *R. o. robustus* the populations that we designate below by the names *R. o. reliquus*, *R. o. oligoporus*, and *R. o. lethoporus*.

SIZE. The fish comprising the five populations of the Lake Diamond drainage system described above differ rather markedly in size (table 20), but no more strikingly than do the populations of the Humboldt River system discussed above (p. 109). The collections from warm springs (Potts Ranch, Dianas Punch Bowl, Birch Ranch, and Big Shipley Spring) are, perhaps by direct environmental response, among the most dwarfed stocks of *Rhinichthys* we have examined. Those from Coils Creek are about as large as *R. o. reliquus* and, among the populations handled, are definitely exceeded in size only by the dace of the Crescent Valley population.

It seems particularly evident that the fish in the hot springs about Dianas Punch Bowl are dwarfed, and are subject to accelerated development, both seasonally and annually. The samples taken in February, 1972, include females as small as 29 mm. with ova already enlarging, though obviously less than one year old. Some in the 3.5 and 4.0 .5-cm. groups had nearly full-formed ova. Males in the 3.0 to 4.0 groups, in part at least surely less than one year old, already had very strongly enlarged paired fins, though none had yet developed the nuptial tubercles on the pectorals.

COLORATION. In general, the coloration corresponds rather well with that of *R. o. robustus* in the Humboldt River headwaters (figs. 22, 23). The primary and secondary bands are apparently somewhat more diffuse. The caudal-base wedge is somewhat more variable and on the average not quite so conspicuous. The blackish stripe on the snout is usually distinct and is subcontinuous with the blackened front part of the upper lip. The speckling on the body is moderately conspicuous in all the series, usually in a rather fine peppery pattern. The specimens from Birch Ranch show a somewhat greater tendency than the others to develop dark horizontal streaks along the scale rows on the side of the trunk. In this series, also, the general pattern is usually more strongly bicolored than in the others, mainly because the lower surfaces are almost entirely silvery on both head and body. In these last two respects the Big Shipley Spring specimens closely approach those from Birch Ranch, with an overlap in variation. The specimens from Coils Creek, perhaps as an environmental effect, are the darkest, and the dark puncticulation tends to extend onto the lower side of the head and sometimes to form a band across the front of the breast. In all five series there is at least a trace of the blackening of the crotches of the dorsal and caudal rays, and in some specimens in the forks of the anal rays.

LIFE COLORS. As noted at the time of collection, none of the specimens at Potts Ranch had bright colors. Some showed orange-gilt reflections over the dark lateral band, and scales, often in patches, stood out sharply with silvery reflections.

The fish at Coils Creek were rather brownish-olive, with a strong wash of golden tan on the mid-sides. The cheeks tended toward gilt, and in some the subopercle was almost orange. In many, the posterior part of the lateral band was orange-gilt. A wide area near the pectoral axil was watery orange-tan. The pelvic axil was watery-salmon in some, but no such color appeared at base of anal, nor about mouth or preopercle. A few had a pinkish speck at the upper end of the gill-opening. Yellowish specks at each end of the dorsal base were not conspicuous. Some were orange-gilt over almost all of the middle and lower sides. One young specimen, 19 mm. in standard length, clearly a mutant, was clear pinkish-yellow, with no dark pattern; its fins were very pale yellow, and its eyes were gilt.

Birch Creek fish, taken the same day, were noted as apparently like those at Big Shipley Spring, which were described as distinctly olive-green (perhaps in response to living in submerged green-leaved vegetation). Blue spangles on scales were particularly bright. The lateral band tended to be tan. The axils of the paired fins were at most very watery-salmon, and there was only a

bare trace of this color at base of anal and upper end of gill-opening, and none at angle of preopercle or about mouth. The cheeks were bluish, not gilt.

FORM. The general form in each set of specimens is rather chubby, probably least so in the Big Shipley Spring and Dianas Punch Bowl series. In all, the mouth is sufficiently oblique for the rostral stripe to include the front of the upper lip. The fins are relatively rounded, as is usual in forms from springs.

BARBEL. The incidence of barbel development in the five populations in the Lake Diamond drainage basin fluctuates somewhat, as it also does in the Humboldt River system (table 11). In three of the five populations, from Potts Ranch, Coils Creek, and Big Shipley Spring, there seem to be about equal numbers of specimens with no barbel, with a barbel on one side only, and with a barbel on each side. The Birch Creek sample, however, includes a high proportion (69 percent) with no barbel on either side. The Dianas Punch Bowl sample shows the strongest development of the barbels, thus seemingly differing from the Potts Ranch sample.

LATERAL LINE. In all five populations the lateral line on the body develops with age well toward completion (table 12, fig. 26). The rate of pore formation as plotted against standard length is least rapid in the least dwarfed population (that of Coils Creek), perhaps because the rate is more dependent on age or state development than on size; yet members of this population finally develop as many. Similarly, among the populations of the Humboldt River system sampled, the one from Crescent Valley is by far the least dwarfed and has the slowest rate of pore development in terms of standard length, yet in the end attains at least as high numbers. At the other Locations in the Diamond system the pore development in the dwarfed stocks is more rapid, apparently in the close-set sequence of Big Shipley Spring, Birch Ranch, Dianas Punch Bowl, Potts Ranch.

SUPRATEMPORAL CANAL. The populations sharply differ in the proportion of specimens with united and interrupted supratemporal canals (bottom entry in table 12). In the Potts Ranch and Big Shipley Spring samples the canal is usually united; in the Coils Creek lot, nearly all are interrupted; in the Dianas Punch Bowl and Birch Ranch lots, these conditions are about equally represented. Similar fluctuations characterize the four samples from the Humboldt River system.

MORPHOMETRY. In proportions, there is wide variation (table 13), with, in general, a broad overlap between the five samples measured, as well as between them and the samples of *R. o. robustus* from the Humboldt River system. There seem to be no very notable differences among the samples within the Diamond system or between these and the Humboldt basin lots in the proportions of the head parts or of the fins.

The feature of the Diamond-system populations that early caught our eyes is a more ample development than is usual of the trunk region, and the compensatory seeming shrinkage of the urosome—features very commonly shown by populations living in springs. The morphometric analysis, however, does not appear to justify subspecific separation. The better development of the trunk region, as expressed by the predorsal proportion, indeed seems sharp when the samples from Potts Ranch and Big Shipley Spring are compared with those from Crescent Valley and Bishop Creek, and significantly, when compared with the sample of transplants taken in a spring in Ruby Valley (further suggesting that the character is gene-dependent). However, the samples from Coils Creek and Birch Ranch in the Diamond system are approximately matched in this respect by the set from springs along Town Creek, a Humboldt headwater, and the specimens from Dianas Punch Bowl are intermediate. The contrast between spring and creek populations is confirmed, but subspecies separability is not.

In the anal-to-caudal proportion there is almost no overlap between the values for either the Big Shipley Spring or the Dianas Punch Bowl series and the Crescent Valley sample, for either sex, but between the other samples there is wide overlap or virtually no difference. The distance

from caudal base to pelvic insertion when stepped forward reaches in the five Diamond-system samples measured to any point between front of orbit and one eye's length before tip of snout (with some sexual dimorphism), but about the same range of variation was noted in samples from the Humboldt River system. The position of the pelvic-fin insertion, as indicated by the serial number of the overlying vertebra (table 17), is essentially similar among the populations from the two drainage systems, with the exception that this measure quantifies a statistically more posterior position of the pelvic fin in the Coils Creek sample, as contrasted with all other series referred to *R. o. robustus*, except those from Carico Lake and Crescent valleys.

The body and caudal-peduncle depths average greater in the Diamond system, except for the Dianas Punch Bowl series, than in the Humboldt basin samples, but the higher values shown by the Ruby Valley transplants suggest that these features are phenotypic.

The head averages larger in the Diamond-system samples, but the proportions are nearly matched by those for the samples from springs near Town Creek and from Ruby Valley.

Sexual dimorphism and nuptial characters. In the position of the dorsal fin and in the length of each fin, the populations of the Lake Diamond system vary widely, with a broad overlap in the values for the populations sampled from the Humboldt River system (table 14). The Big Shipley Spring sample is remarkable in not showing the usual backward location of the dorsal fin in females, yet is distinctive in having, in males, among all samples analyzed from both systems, the greatest relative enlargement of the pectoral fin (but not of the pelvic). However, the index value is almost as large in the Dianas Punch Bowl fish, which, oddly, exhibit stronger dimorphism in fin size than those from Potts Ranch nearby. Insofar as exhibited, the nuptial tuberculation (fig. 23B) agrees with that described for the species (p. 98).

Fin rays. For none of the fins are the differences in ray number between samples within the Diamond system or between these samples and the ones for the Humboldt system, as shown in table 15, of subspecific significance. There are some suggestions of the trend toward a reduced number in the spring-inhabiting populations. This is hardly shown for the dorsal and anal rays. For pectoral rays there is probably a slight numerical reduction in the Coils Creek and Dianas Punch Bowl samples, as also in the set from springs near Town Creek (a Humboldt headwater), and a small but seemingly definite reduction in the three other samples from the Diamond system. For the pelvic rays there seems to be a slight reduction for the series from springs near Town Creek, oddly for the Ruby Valley transplants, and for the Dianas Punch Bowl and Coils Creek samples, and a more definite statistical reduction in the three other series from the Diamond Valley complex.

Vertebrae. The total vertebral numbers (table 16) show only a very slight and very irregular trend toward reduction in the populations from the Lake Diamond drainage system, and some odd, slight fluctuations among the samples from the Humboldt River system.

Scale rows. Within each drainage basin, the counts for four scale rows (table 18) constitute a cline, as follows:

For the Diamond basin: (Big Shipley Spring or Birch Ranch) < Potts Ranch < Dianas Punch Bowl (except for rows around peduncle) < Coils Creek.
For the Humboldt basin: Bishop Creek < Ruby Valley < springs near Town Creek < Crescent Valley (with a shift in position for rows around caudal peduncle between springs near Town Creek and Ruby Valley).

Between the two extreme samples of the two categories (low counts for Big Shipley Spring or Birch Ranch and high counts for Crescent Valley) there is almost no overlap for the predorsal series or for rows around caudal peduncle, and only a moderate overlap for the lateral-line and around-body series. The three specimens from Carico Lake Valley had the highest count for lateral-line scales, but median values for the other series.

GILL-RAKERS AND PHARYNGEAL TEETH. For the numbers of gill-rakers (table 18) and teeth no notable differences were found between samples within the Lake Diamond drainage basin, or between those and the series counted from the Humboldt River system.

SEXUAL DIFFERENCES IN NUMBERS, BIOMASS, AND SIZE (tables 19, 20). In strong contrast to the samples from the Humboldt system, those representing the five isolated populations of the Diamond system vary spectacularly in sex ratio, in terms both of numbers and of biomass: the ratio of males per 100 females varies from 25 in the Big Shipley Spring sample to 124 in the Potts Ranch collection. The ratio (M/F) in terms of biomass varies, in essentially the same sequence, but to an exaggerated degree, from .12 to 1.10.

The sexual discrepancy in size also varies. In the Potts Ranch, Dianas Punch Bowl, and Birch Ranch series, the males and females are both dwarfed, and only 30, 6, and 17 percent of the females, respectively, are in .5-cm. size groups larger than any containing males, suggesting that most individuals may be yearlings (the ages of the fish were not determined). In the Big Shipley Spring sample the males are about as small as in these three sets, but 45 percent of the females are in size classes larger than any containing males—suggesting a considerable number of a greater age. In the Coils Creek series both sexes are larger, indicating better growth, and 15 percent of the females are in size groups exceeding the largest for males.

GRASS VALLEY SPECKLED DACE

Rhinichthys osculus reliquus Hubbs and Miller.

(Figure 24A,B.)

Rhinichthys osculus reliquus HUBBS and MILLER, 1972, p. 104 (diagnosis).

This subspecies of *Rhinichthys osculus*, one of the most distinctive, was, until its almost certain recent extermination, confined to Grass Valley, the depression that constituted the drainage basin of pluvial Lake Gilbert (pp. 10–14, fig. 2), near the middle of the northern border of the Great Basin, in central Nevada. It apparently was the only kind of fish that survived in the basin until modern time, though there are reasons (see below) to believe that *Gila bicolor* also occurred there at some Pleistocene time. The subspecies is known from a single collection, with the following data:

Location R9.—Spring-fed creek in a grassy meadow in the partly enclosed southwestern arm of **Grass Valley**, 13 km. east of Mt. Callaghan, in the course of Callaghan (Woodward) Creek, on Grass Valley Ranch, in SW ¼, Sec. 10, T. 21 N., R. 46 E. (see U. S. G. S. Mount Callaghan 15-minute quadrangle); in eastern Lander County, Nevada (fig. 3). Clear water; soft mud; slight to moderate current; generally choked with *Nasturtium*, *Chara*, bulrushes, etc.; 19° C. (air 25°). Hubbs family and Miller, August 9, 1938 (M38–116); UMMZ 124906–07 (474, 12–82 mm.); 15-foot seine with ¼-inch square mesh.

In 1938 the dace here were common and large. Dick McGee, then owner of Grass Valley Ranch, said that trout are frequently stocked in springs and creeks on the ranch, and we saw one where we collected.

We found no evidence that dace occurred elsewhere in the basin of pluvial Lake Gilbert (p. 14).

Inasmuch as a local form of *Gila bicolor*, as well as one of *Rhinichthys osculus*, occurs in Big Smoky Valley, the basin of pluvial Lake Toiyabe, which apparently obtained its fish fauna from Grass Valley through piracy of a southern tributary of that valley (pp. 14–15), it seems probable that *Gila bicolor* formerly existed in the basin of Lake Gilbert but failed to survive there.

The physiographic evidence strongly suggests that this relict was derived from the Lahontan basin subspecies, *Rhinichthys osculus robustus*, or its ancestor. That subspecies was found to abound in Crescent Valley, into which Lake Gilbert is assumed to have discharged, probably at an early pluvial period (pp. 11 and 107), and Crescent Valley retains, at high-flood stages, a connection with the Humboldt River (p. 107).

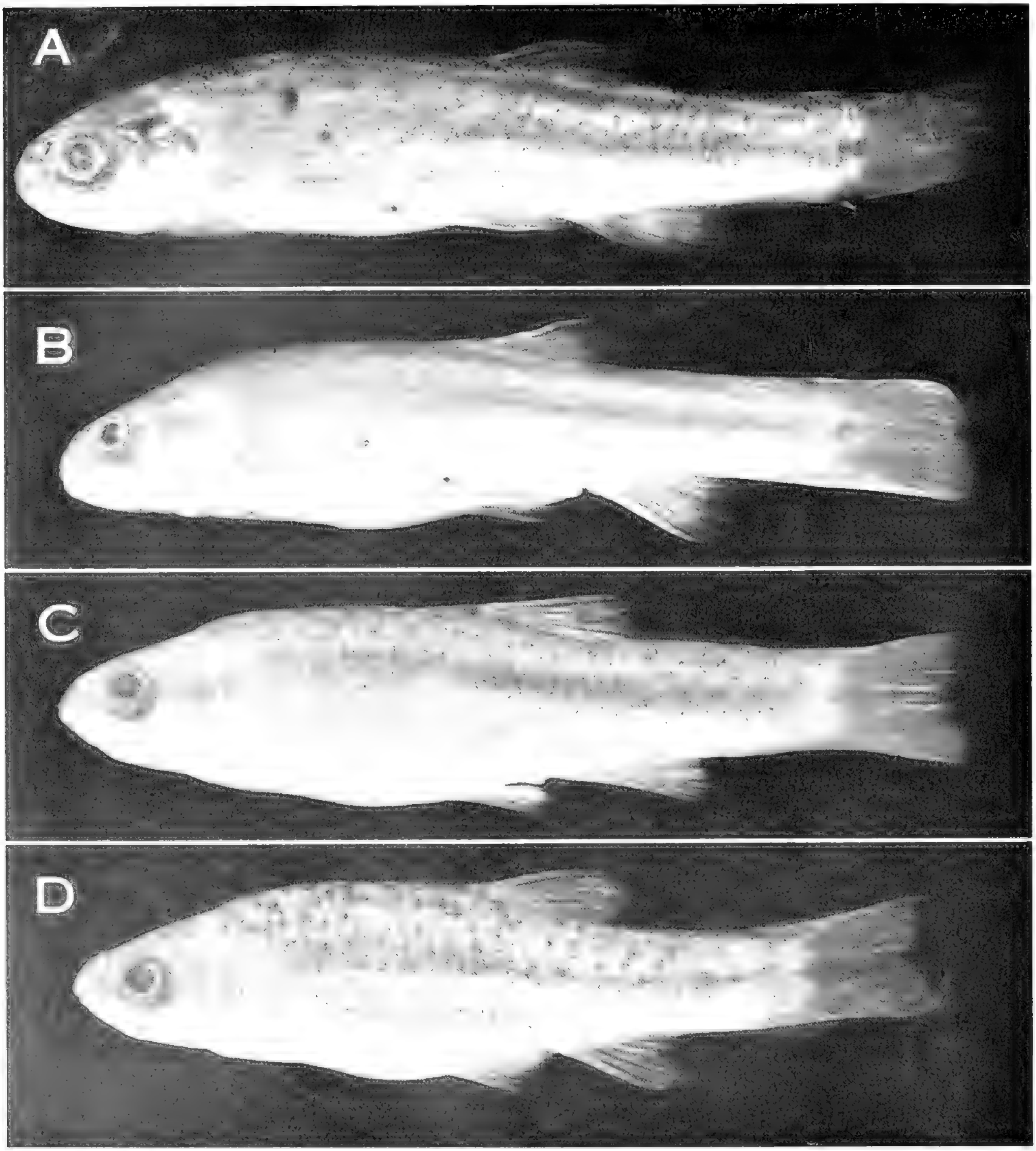


FIGURE 24. Two subspecies of *Rhinichthys osculus*, from Grass and Independence valleys, Nevada. A. *R. o. reliquus*, Grass Valley (Location R9); UMMZ 124907, no. 23; paratype, male, 46.0 mm. B. *R. o. reliquus*, same field collection; UMMZ 124906; holotype, female, 67 mm. C. *R. o. lethoporus*, Independence Valley (R12); UMMZ 186519, no. 13; paratype, male, 34.1 mm. D. *R. o. lethoporus*, same field collection; UMMZ 186905; holotype, female, 35.3 mm.

However, the highly distinctive characters of *R. o. reliquus* lead us to entertain the thought that it might be a relict, which represents some early, unknown ancestor (see also p. 14).

Apparent Extinction.

When the ditches and the main spring on Grass Valley Ranch were examined by the Miller family in August, 1969, in an effort to obtain material of this dace for chromosome study, no trace of it could be found, despite an all-day effort. Only rainbow and brook trout, *Salmo gairdnerii* and *Salvelinus fontinalis*, were located, and the present rancher, Mrs. Knutson (formerly Mrs. Dick McGee), mentioned knowing of large rainbow trout below Grass Valley Ranch and of both species on and above the ranch. Mrs. Knutson knew of the former existence of the dace, and thought that it might be extant in a large spring in the meadow of Callaghan Ranch, about 10 km. upstream, but we found none there. We have since received confirmatory indication of the extinction of this dace from Dr. Ira La Rivers (personal communication, Dec. 9, 1969), who has written us that "I was there some ten years ago trying to get the native dace and it was gone then, as far as I could determine, and the stream was full of trout." He also talked with Mrs. Knutson, and added: "I am sure the dace are gone from this particular locality." Furthermore, a recent effort to locate dace in Grass Valley was unsuccessful (Thomas P. Lugaski, personal communication, 1972). Apparently we have described *R. o. reliquus* posthumously, following an unhappy precedent that we established in an earlier publication (Miller and Hubbs, 1960, pp. 21–23, 27–28, 56).

Description and Comparisons.

Holotype, UMMZ 124906, an adult female 67 mm. in standard length (fig. 24B). Paratypes 124907, all other known specimens (473, 12–82 mm. long) from same Location (R9, data given above), including the adult male, 46.0 mm. long, that is illustrated (fig. 24A).

The osteological characters attributed to *Rhinichthys* in the description of the genus *Relictus* (pp. 182–193, figs. 38–45) are based primarily on preparations of *R. o. reliquus*.

In the following account, *R. o. reliquus* is compared primarily with the population of *R. o. robustus* that occupies Indian Creek in Crescent Valley. The distinctions, however, apply also to other populations of that subspecies, including those of Bishop Creek and springs near Town Creek (pp. 105–121).

This form is so trenchantly distinctive in comparison with the others herein treated that we think it may seem worthy of species rank when a sufficient number of other local differentiates has been analyzed.

Size. Although *Rhinichthys osculus reliquus* is one of the forms restricted to an isolated spring-fed area, it is not dwarfed (table 20), but rather, according to our mass collections, reaches the largest size (82 mm.) of any of the forms of *R. osculus* considered in this report, with the exception of the population of *R. o. robustus* that occupies Indian Creek in Crescent Valley.

Coloration. In general appearance (figs. 24A,B) this subspecies is quite different from *R. o. robustus*, because the body usually is less speckled: the blackened regenerated scales are rather fewer and less emphasized and the underlying main dark lateral band is generally broader, more solid, and more even-edged. The pattern is further intensified by the more definitely lightened ground color between this lateral band and the dark, broad predorsal stripe. The lower sides, especially posteriorly, are often marked with deep-lying giant melanophores, which are more conspicuous than in *R. o. robustus* and form puncticulations somewhat similar to those on this region in the subgenus *Siphateles* of *Gila*. The lower dark lateral band, which is usually rather well developed in *R. o. robustus*, and which in *R. o. lariversi* Lugaski of Big Smoky Valley usually is evenly pigmented and strongly deflected downward toward or to the anal base, is obsolescent in *R. o. reliquus*. Very distinctive of *R. o. reliquus* is a dark streak or wedge along the lower

border of the caudal peduncle (it fades in some large individuals). The head is characteristically darkened from the suborbital region, where the dark area is broad, and from the front part of the mouth, upward and backward over the front and top of the head (whereas in the other forms here treated, the dark area does not extend so far below the eye and on the snout tends to form a horizontal dark stripe, which is barely even suggested in *R. o. reliquus*). The vertical fins also are more uniformly darkened, and less speckled, than in *R. o. robustus*, with hardly a trace of the especial blackening at the bifurcation of the rays. In this respect there is better agreement with the forms here called *R. o. oligoporus* and *R. o. lethoporus*. In general, however, the color pattern suggests that of *R. o. robustus*.

Another distinctive feature of *R. o. reliquus* involves the pigmentation of the lower lip: even when the lower surface of the head is elsewhere devoid of pigment, the lower lip is heavily punctate all around. In the populations herein referred to *R. o. robustus*, even in the occasional specimens that are heavily punctate over the lower surface of the head elsewhere, the lower lip, in strong contrast, remains immaculate, save occasionally for a small dash near end of gape, and very rarely for partial pigmentation around the front rim of the lip. There is a slight tendency for the character to break down in the Coils Creek population (referred to *R. o. robustus*) and in *R. o. lariversi* of Big Smoky Valley, and in this character *R. o. lethoporus* (but not *R. o. oligoporus*) is intermediate.

Life colors. The field records indicate that the life colors may also be somewhat distinctive. The red color that is often apparent in the axils of the paired fins of the species was barely represented, in that some individuals had the axils of the paired fins and the base of the anal at most rather brownish red, seldom at all conspicuous. In further contrast with many populations of *Rhinichthys osculus*, there was no red about the mouth or preopercle and only occasionally a mere trace at the upper end of the gill opening. However, the lack of red may have been due to the postnuptial condition of the specimens. The sides were silver-spangled on individual scales, but the general tone was brownish olive. The cheeks showed gilt and blue reflections in some individuals. The field notes further indicate that the general impression of this dace in life approached that of *Relictus solitarius*.

Form. *Rhinichthys o. reliquus* contrasts with *R. o. robustus* in having the body more turgid in the nuchal region and in having the muzzle more rounded, more declivous, and broader, so that the overall width of the mouth approximately equals instead of being shorter than the snout. As seen from below, the mouth is very broadly U-shaped, instead of being narrower, approaching a V. These distinctions tend to break down slightly when *R. o. reliquus* is compared with the isolated populations of the Diamond Valley drainage, but hold well in comparisons with the populations from Indian Creek in Crescent Valley and from Bishop and Town creeks in the extreme headwaters of the Humboldt River drainage basin.

Frenum. Among 100 specimens of each sex specifically examined for this structure, none had the rostral groove interrupted by a fleshy bridge on the midline; in one specimen the groove was shallow.

Barbel (table 11). *Rhinichthys o. reliquus* is further distinguished by the virtually invariable lack of a barbel. Among 100 specimens of each sex carefully checked, only one has a very minute barbel, on one side. In all populations here referred to *R. o. robustus*, a considerable proportion of the specimens (a majority for all samples except that from Birch Ranch) have a barbel on either one or both sides. The complete or almost complete lack of a barbel on either side otherwise characterizes *R. o. oligoporus* and *R. o. lethoporus* (pp. 100 and 104).

Lateral-line system (table 12, figs. 25, 26). Despite the fact that it is by no means dwarfed, this form, along with *R. o. oligoporus* and *R. o. lethoporus*, is characterized by an extreme reduction in the development of the lateral line on the body.

The lateral-line system is also degenerate on the head. All 40 specimens checked had the supratemporal canal commissure interrupted medially, typically very widely.

Scale structure. The scales show the typical structure of *Rhinichthys* (p. 97).

Morphometry (table 13). The morphometric measurements provide relatively little that is sharply distinctive of this subspecies. The body averages slenderer than in other forms. The depth of the caudal peduncle is less than that of *R. o. lethoporus*, with only a slight overlap, but is about average for *R. o. robustus* and *R. o. oligoporus*. The head length and the eye length are not markedly distinctive, except that they are proportionally shorter than in *R. o. lethoporus* (in correlation with the extreme dwarfing of that subspecies). The head depth and width and the snout length are about average. The interorbital width is on the low side. The suborbital width is about the same as in most of the other populations, but averages greater than in *R. o. lethoporus* (again in correlation with the dwarfing of that form). The fin lengths are on the low side, but only on the average, and, as is usual in spring-inhabiting minnows, the fins are rounded.

The position of the fins (table 13) provides some distinctions. The predorsal length is high on the average, but variable: in the adult males about the same as in the Big Shipley Spring population, but somewhat greater than in the others; in the females, close to the means of all other populations sampled. The distance from anal origin to caudal base is definitely lowest in each sex, but with wide overlap. Very distinctively, the pelvic fin is more posteriorly inserted in *R. o. reliquus* than in any other form here considered (including *R. o. lariversi* of Big Smoky Valley). This distinction can be shown in two ways: (1) the distance when measured forward extends, with little variation, about to middle of eye in *R. o. reliquus*, but about to tip of snout in the other forms, with considerable variation; (2) the pelvic insertion, as seen on radiographs, usually lies in *R. o. reliquus* below a more posterior vertebra (table 17), but this measure of the position seems to be less consistent than is indicated by the first method and is somewhat subjective.

Sexual dimorphism and nuptial characters. The sexual dimorphism in the length of the pectoral fin in this subspecies is more extreme than in any of the other populations treated (table 14), more because of shortness in females than of extra length in males: on the average the fin is 6.7 percent of the standard length longer in males than in females. The extreme excess length in males does not hold for the pelvic fin. The dorsal and caudal fins on the average are larger, but not quite so extreme. The dorsal fin is, on the average, even more posteriorly inserted in males than in females, contrary to the situation in the species as a whole, and in cyprinids in general.

The pectoral fin in males has very thick and firm rays. The adult males, taken probably past the peak of nuptial activity, have, as is usual in the species, the outermost, unbranched pectoral ray and the two or three following branched rays strongly dilated and more or less curved. The first ray seems to have been considerably padded, but in the specimens at hand is devoid of nuptial tubercles. The tubercles, one per segment, seem to have been confined mostly or entirely to the first few strengthened branched rays. It could not be ascertained definitely whether the single row of tubercles branches once, as it often does in *R. osculus*.

Fin rays (table 15). The counts of dorsal and anal rays average very slightly higher than in the other populations: contrary to the general rule for *R. osculus*, counts above 8 in the dorsal fin and above 7 in the anal fin exceed those below these numbers. The pectoral-ray counts average fewer than in any of the populations of *R. o. robustus* treated (except for the set of 3 specimens from Carico Lake Valley), but about the same as in *R. o. oligoporus* and *R. o. lethoporus*. The pelvic-ray numbers average slightly lower than in *R. o. robustus*, but barely less than in some of the isolated colonies in the Diamond Valley drainage basin, and very slightly higher than in *R. o. oligoporus* and *R. o. lethoporus*.

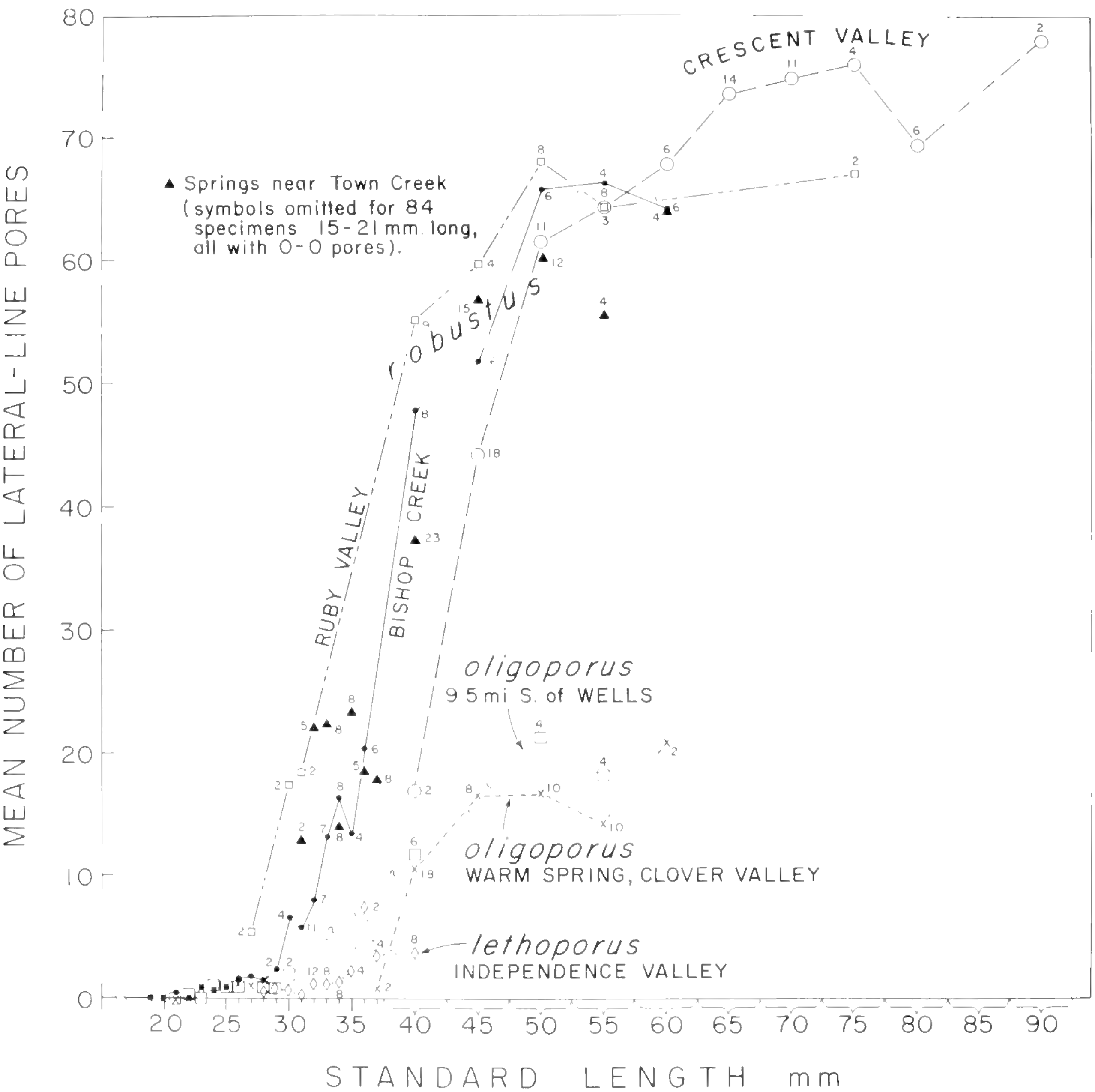


FIGURE 25. Development of lateral-line pores on body in subspecies of *Rhinichthys osculus* from headwaters of Humboldt River and from basin of pluvial Lake Clover, Nevada. Numerals beside symbols indicate numbers of sides counted (omitted on entries for specimens less than 32 mm. long having pore-number average less than 2.0). Data from table 12.

VERTEBRAE (table 16). The precaudal vertebrae average moderately to very slightly higher than in the populations referred to *R. o. robustus* (the Carico Lake Valley set of three specimens excepted) and *R. o. lethoporus*, but not higher than in *R. o. oligoporus*. The caudal vertebrae, however, definitely average fewer than in the other forms (though hardly different from one population of *R. o. oligoporus*); this is surprising, in view of the more posterior position of the anal

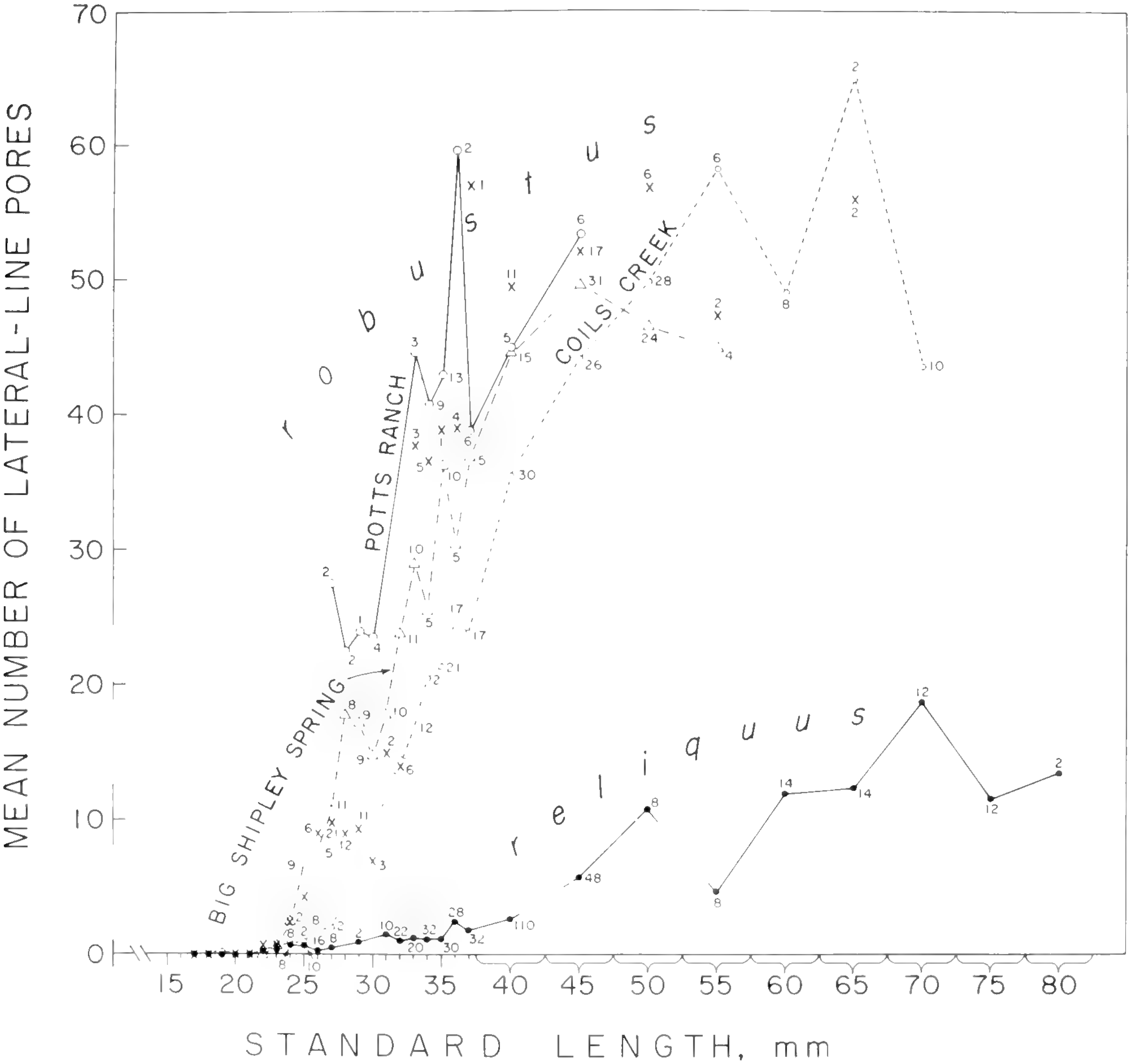


FIGURE 26. Development of lateral-line pores on body in populations of *Rhinichthys osculus robustus* from basin of pluvial Lake Diamond, and in *R. o. reliquus* of Grass Valley (basin of Lake Gilbert), Nevada. The crosses (not interconnected) represent the values for Birch Ranch. Numerals beside symbols indicate number of sides counted (omitted on entries for specimens less than 24 mm. long having pore-number average less than 1.0). The values for Dianas Punch Bowl Springs, not plotted, approximate those for Potts Ranch or Big Shipley Spring. Data from table 12.

and especially of the pelvic fin in *R. o. reliquus*. Because the higher average for precaudal counts is less than the lower average of caudals, the total number averages barely lower in *R. o. reliquus* than in some populations of the other subspecies.

SCALE ROWS (table 18). The four counts, namely lateral-line series, predorsal rows, around body, and around caudal peduncle, average consistently higher than in the two dwarfed subspecies (*R. o. oligoporus* and *R. o. lethoporus*),

TABLE 14. *Sexual dimorphism in predorsal and fin lengths in populations of* Rhinichthys osculus *in certain basins in Nevada, expressed as excess for males over females in mean values in permillage of standard length.*[1]

Subspecies Pluvial lake system Locality	Predorsal length	Dorsal fin	Caudal fin	Pectoral fin	Pelvic fin
R. o. robustus					
L. Lahontan (Humboldt R.)					
Crescent Valley (10/10)[2]	−13	8	15	39	20
Bishop Creek (7/12)	−19	24	14	46	25
Springs near Town Cr. (20/20)	−14	8	10	43	16
L. Franklin (introduced)					
Ruby Valley (4/7)	−19	7	14	48	26
L. Diamond					
Potts Ranch (10/10)	−10	0	(−11)[3]	38	9
Dianas Punch Bowl (10/10)	−10	21	12	55	21
Coils Creek (20/20)	− 7	14	10	52	19
Birch Ranch (20/20)	−17	16	20	44	22
Big Shipley Spr. (15/21)	1	22	19	57	12
R. o. reliquus					
L. Gilbert					
Grass Valley (20/20)	7	21	19	67	16
R. o. oligoporus					
L. Clover					
9.5 mi. S. of Wells (3/4)	4	28	52[4]	53	26
Warm Sprs., Clover V. (12/15)	−18	26	21	43	28
R. o. lethoporus					
L. Clover					
Independence Valley (12/12)	− 1	18	7	52	9

[1] Based on values in table 13.
[2] Figures in parentheses indicate the number of adult males and adult females, respectively, that were measured; a few fin measurements were missed.
[3] Only 3 measurements for males and only 1 for females.
[4] Only 2 measurements for males and only 1 for females.

with relatively little overlap. Almost all averages are also higher than in the populations of *R. o. robustus* studied, except for the collections from Crescent Valley.

GILL-RAKERS (table 18). The rakers may average slightly lower in number than in the other populations here analyzed, except for those comprising the type series of *R. o. oligoporus* and for the set of three specimens from Carico Lake Valley.

PHARYNGEAL TEETH. In all 20 specimens examined the tooth formula was interpreted as 1, 4—4, 1, by including in the count what appear to be alveoli of lost teeth, especially in the lesser row (only one such alveolus was largely filled in by bone).

SEXUAL DIFFERENCES IN NUMBERS AND BIOMASS (tables 19, 20). The type collection of *R. o. reliquus*, the only one obtained, comprises, young included, 183 males 12 to 47 mm. in standard length and 291 females 17 to 82 mm. long, a ratio of 63 males to 100 females. The discrepancy by volume is even greater, 136 to 498 ml., a ratio of .27:1. Since the sample was collected with a seine having a 1/4-inch square mesh, most of the young, which were presumably abundant on August 9, no doubt escaped. Females of the 0 age-group were mostly in the 2.0- and 2.5-cm. size-classes, which graded into the adult size-classes. Since the adult males were small, the young males did not form a distinct mode. The size-class frequencies suggest that the adult males were almost all yearlings, whereas the skew size distribution for females, with modes at the 3.5–4.0 and at the 6.0–6.5 cm. size-classes, suggests that a considerable proportion of the females were two years old.

DERIVATION OF NAME. The meaning of *reliquus* is given as "that is left behind, or remains."

Clover Valley Speckled Dace

Rhinichthys osculus oligoporus Hubbs and Miller.

(Figure 27.)

Rhinichthys osculus oligoporus Hubbs and Miller, 1972, p. 105 (diagnosis).

This is one of the two spring-inhabiting subspecies of *Rhinichthys osculus* that we recognize from the basin of pluvial Lake Clover, which occupied the broadly connected Clover and Independence valleys, in northeastern Nevada (pp. 29–32; figs. 8, 11, 12). The second form is *R. o. lethoporus*, described below, from a spring in Independence Valley.

We refer to *R. o. oligoporus* two slightly differentiated forms, from separate springs, both in Clover Valley, near the western edge of the ancient lake bed. These spring waters were treated by Eakin and Maxey (1951b), with chemical analyses of Warm Springs.

Location R10.—Spring pond and outflow **9.5 miles south of Wells**, issuing from near an outcrop of lava at the southeastern base of a juniper-covered hill, near the north end of the western border of the flat bottom of Clover Valley, near corner of Secs. 19–20 and 29–30, T. 36 N., R. 62 E. (see Elko 1:250,000 map); east of center of Elko County, Nevada (fig. 12). Two collections were made, under different conditions:

First collection, in spring-head reservoir about 3 m. deep and about 1 acre in extent, and in the outlet, on what was then known as Ralph Ranch. At that time the pond was bordered on one side by a wooded slope and on the other side by a grassy meadow. Clear water; rather firm, whitish bottom; current moderate in outlet; choked with *Potamogeton*, cf. *P. pectinatus*, *Chara*, etc.; water cool. Hubbs family, September 14, 1934 (M34–213); UMMZ 132192–93 (94, 14–40 mm.); 6-foot woven-mesh seine and 15-foot seine with ¼-inch square mesh. On this occasion, in the year of excessive drought, this spring, the largest in the valley north of "Clover Ranch" (now Warm Springs Ranch, Location R11), was the only source of water at this major ranch, since snow water from the East Humboldt Range had failed, and the extensive meadows had "burned up."

Second collection, in the southernmost of the ditched outlets, with one haul in the headwater reservoir, now largely silted-in and surrounded by dense woods, on the property now called Wright Ranch. Water clear, but very easily muddied; bottom now of deep mud; dense growth of *Potamogeton*, cf. *P. pectinatus*, and a sparse growth of a floating filamentous green alga; 17.2–17.8° C. (air 24°). Miller family and the Hubbses, August 26, 1965 (M65–35); UMMZ 186521 (102, 14–55 mm., including the female figured); 12-foot woven-mesh seine.

When these spring waters were examined in 1934, the dace were scarce and mostly very small, apparently because they had been preyed upon by large rainbow trout, *Salmo gairdnerii* (one seen), and because the water had been used for irrigation of the hay meadows. Diligent collecting produced only young fish and a single adult. The rancher (Mr. Ralph) informed us that previously the minnows had been more abundant and had reached a larger size. In 1965, a year of heavy precipitation, water was more profuse, and trout were not in evidence. The population of dace had recovered, and adults were not so extremely scarce.

Location R11.—**Warm Springs, Clover Valley**, at Warm Creek (formerly Clover) Ranch, near southeastern corner of Clover Valley, near foot of bajada just above the flat ancient bed of Lake Clover, in Sec. 7, T. 33 N., R. 61 E. (see Elko 1:250,000 map); in southeastern Elko County, Nevada, at east side of U. S. Highway 93, 3.1 miles north of junction with State Highway 11 (figs. 8, 12). The main spring was said by the owner of the ranch, in 1965, to deliver 3,200 gallons per minute. Two collections were made:

First collection, in the outlet of the deep spring-fed reservoir. Water clear; gravel, mud, and debris; vegetation dense; 18.5° C.; width to 3 m. and depth to 0.6 m. James E. Deacon and Mary Beth Rheuben, September 14, 1964 (JED 64–55); UMMZ 186902 (holotype, 55.2 mm.) and 186903 (29 paratypes, 15–58.5 mm.); 15-foot seine with ¼-inch square mesh.

Second collection, in a very short lateral inlet flow, 0.3 to 1.0 m. wide, of the reservoir. Water very clear, but easily muddied; silt over gravel, rocks, and firm mud; current barely perceptible; largely choked with *Nasturtium*, with some fine-leaved submergent, and some *Chara* toward spring head; 19.3° C. (air 25°). Miller family and the Hubbses, August 26, 1965 (M65–34); UMMZ 186520 (88, 12–28 mm.); 6-foot woven-mesh seine.

When this spring, then known as Clover Spring, was first examined by us, on September 14, 1934,

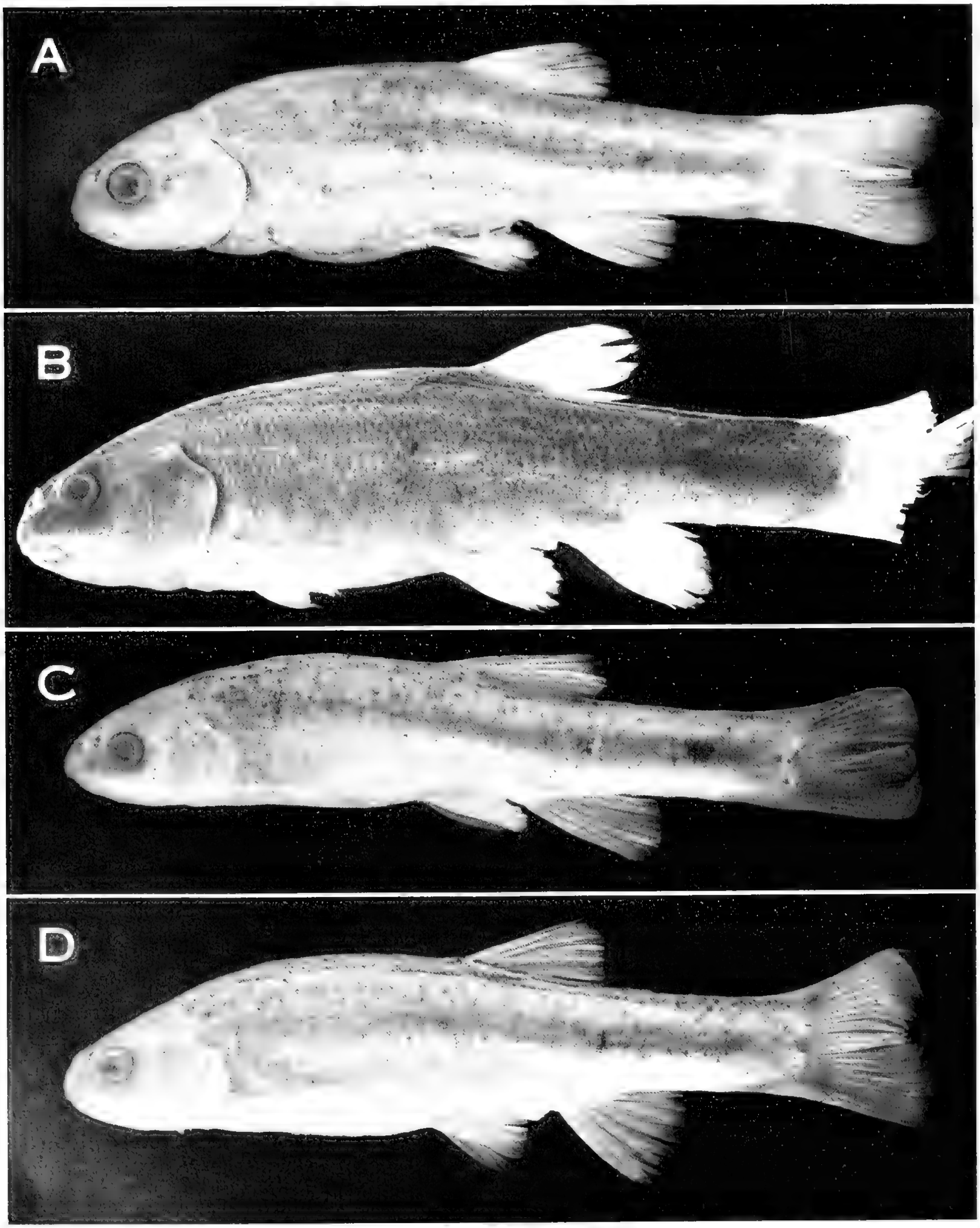


FIGURE 27. *Rhinichthys osculus oligoporus*, from Clover Valley, Nevada. A. South of Wells 9.5 miles (Location R10, first collection): UMMZ 132192, unnumbered specimen: male, 39.9 mm. B. Same Location (second collection): UMMZ 186521, no. 1: female, 55.4 mm. C. Warm Springs (R11, first collection): UMMZ 186903, no. 18: paratype, male, 44.2 mm. D. Same field collection: UMMZ 186902: holotype, female, 55.2 mm.

the rancher said that it has a temperature of 55° F. (13° C.) and is fishless, but he may have thought of game fish and was, almost uniquely in our Great Basin experience, definitely inhospitable and uncooperative. Although we saw no fish in this spring, the possibility seems to us rather remote that the dace were actually absent in 1934. One reason for so thinking is that the only reasonable source of dace for stocking would have been from Ralph Ranch (Location R10), which is on the same road, the only one on the western side of the valley, or in an immediately adjacent locality, and the two stocks seem to be somewhat differentiated. Furthermore, the dace may have been in seclusion in the ponded spring water, just as *Relictus solitarius* apparently was on the same day near Currie, following a night when water froze in camp (p. 204).

When the first collection was made, just 30 years to the day after our first visit to the spring, Dr. Deacon observed a sizable population in the deep reservoir, and the rancher said that the minnows abounded in the pond. He refrained from collecting there because the rancher did not want him to disturb the rainbow trout, which had been stocked recently, and had reputedly doubled in size over the summer. For this reason, the collecting was confined to the outlet ditch, where the dace were scarce, as also in the distributaries in the meadow. When we examined the spring about a year later, making the second collection, we saw no trace of dace in the clear water of the reservoir, in the main spring inlet issuing (at side of highway) from just above the bajada base, in the main outlet ditch from the impoundment, or in the smaller springs and overflows on the meadow below. The only place where fish were found, after prolonged search, was in a slight lateral inflow, tributary to the main inlet between the spring source and the reservoir, and here only young fish were encountered. It appeared that the introduced rainbow trout were forcing the localized form of speckled dace definitely into the seriously endangered category. Bullfrogs, *Rana catesbeiana*, found in 1965 to be common, may have contributed to the decimation of the dace.

We assume that this local form, as well as *R. o. lethoporus* of Warm Springs in Independence Valley, the next subspecies, was derived from the stock of *R. o. robustus*, or its ancestor, in the headwaters of the Humboldt River immediately to the north. The indication has already been presented (pp. 30–31) of a presumably Pleistocene, but not latest Pleistocene age, outflow from pluvial Lake Clover into the Humboldt River headwaters. The marked differentiation of these two subspecies from *R. o. robustus* of the upper Humboldt River system and the slight differentiation of the two from one another (as specified in the account of *R. o. lethoporus*), and the slight distinction between the two populations of Clover Valley (Locations R10 and R11), specified below, are compatible with this physiographic evidence.

Warm Springs in Independence Valley have presumably long been isolated from the habitats of *R. o. oligoporus*, and neither a field reconnaissance nor a scrutiny of the Elko 1:250,000 map has yielded any plausible present-time floodwater connection, although the flood channel from Location R10 for *R. o. oligoporus* runs into the alkali flat of Independence Valley. The channels in Clover Valley, however, appear to be braided, and it is possible that at times flood water discharges from Location R10 have reached either the impounded waters or a flood overflow of ephemeral Snow Water Lake, which is fed by the discharge of the Warm Springs of Clover Valley (R11). No such ephemeral lake exists in Independence Valley. Hence it is plausible to assume that the two populations treated as one subspecies (*oligoporus*) have been connected after the Independence Valley form (now modified as *R. o. lethoporus*) was separated, but it seems improbable that such connection has been recent. (In interpreting the 1:250,000 maps involved—Elko and Wells—it needs to be kept in mind that the 5,600-foot contour in Independence Valley

and the 5,700- and 5,800-foot contours in both valleys were inadvertently not marked as enclosed.)

Description and Comparisons.

Holotype, UMMZ 186902, an adult female 55.2 mm. in standard length (fig. 27D). Paratypes, 186903 (29, 15–58.5 mm. long). The specimens designated as types comprise all taken in only the first of the two collections described above for Location R11, including the mature male, no. 18, 44.2 mm. long, that is illustrated (fig. 27C).

We compare this subspecies, one of the spring-inhabiting forms of *R. osculus*, primarily with the upper Humboldt stocks of *R. o. robustus. Rhinichthys o. reliquus* is distinguished above from this form, and the distinctness of *R. o. lethoporus* is detailed in the next subspecies account. *R. o. oligoporus* seems to be much less sharply differentiated than *R. o. reliquus*, and somewhat less modified than *R. o. lethoporus* (of the same basin).

Size. Although relatively few adults were obtained, this subspecies appears to attain about average size for *R. osculus* (table 20).

Coloration. In comparison with *R. o. robustus* (figs. 22, 23), the body in this subspecies (fig. 27) is more extensively speckled with black. The lower lateral band as a rule is much less developed, or not evident; the dark pigmentation around the snout is more generally diffused, with virtually no evidence of the usual horizontal black streak in front of the eye, but retaining a tendency for its continuation across the opercle that is characteristic of *R. o. robustus*. The jet-black wedge that is ordinarily developed at the base of the caudal on the midline in *R. o. robustus* is much smaller, less intense, and more disrupted, and occasionally hardly evident. Dusky dashes on the dorsal and caudal fins tend to be more numerous than in *R. o. robustus*, but are virtually unrepresented on the anal fin, where they are rather often developed in *R. o. robustus*. These marks are much less apt to form in, and to be largely restricted to, the crotches of the bifurcating rays. The preserved specimens as well as individuals in life (see below) have a light streak, bordering the main lateral band above, that is hardly evident in *R. o. robustus*. Despite these various differences, the general coloration of the two subspecies has many features in common. Many of these differences tend to break down somewhat when comparison is made with the five populations from isolated parts of the Diamond Valley drainage system.

Life colors. The only field notes on color, taken at the first collection at Location R10, indicate that the population there is bright olive or golden green on the back and silvery below, with an intervening bright gilt stripe and with dusky mottling. The only adult taken here, a male, unlike the specimens of *R. o. reliquus*, displayed clear red in the axils of the paired fins and along the base of the anal.

Form. In comparison with *R. o. robustus* (figs. 22, 23), *R. o. oligoporus* (fig. 27) differs in general form. The outlines of the body, and especially of the head, are more curved, and the head in particular is more rounded, in both dorsal and lateral aspects. The mouth tends to be more definitely lower than the lower border of the eye, and is generally more curved. The whole aspect is bulkier.

Frenum. Not one of the specimens was observed to have a frenum.

Barbel (table 11). In this subspecies, like *R. o. reliquus* and *R. o. lethoporus*, the obsolescence of the barbel that is often evident in isolated stocks and derivatives of *R. o. robustus* has been carried almost if not completely to the degree of total absence. Not one of the 51 specimens, about equally from both Locations, that were checked, on both sides, shows any trace of this sensory structure.

Lateral-line system (table 12; figs. 25, 26). Perhaps in correlation with its isolation, this subspecies, along with *R. o. reliquus* and *R. o. lethoporus*, is characterized by an extreme reduction of the lateral line on the body. In this respect the

two populations referred to this subspecies are not markedly different.

The lateral-line system is also degenerate on the head. The numbers of specimens with a united and an interrupted supratemporal canal (table 12), respectively, are 3 and 3 for Location R10, and 14 and 1 for R11, suggesting some local differentiation.

SCALE STRUCTURE. The scales show the typical structure of *Rhinichthys* (p. 97).

MORPHOMETRY (table 13). The morphometry of *R. o. oligoporus* is not sharply distinctive. The specimens from Location R10 are among the deeper-bodied of those from all the collections considered, whereas those from R11 are among the slenderer. This difference may be phenotypic. Caudal-peduncle depth is about average. Perhaps because of the small sample, or because of differential nutrition, the three adult females from Location R10 have the head deeper and wider than do the four adult males from the same place, or in the adults of either sex from R11. The suborbital seems to average slightly narrower than in other populations of the species examined, *R. o. lethoporus* excepted. Otherwise, the dimensions of the head parts seem to be about average. The size of the fins is also about average. As in the other forms under discussion, the fins are relatively small and rounded.

The position of the dorsal and anal fins (table 13) is not distinctive among the forms of *Rhinichthys osculus* here treated, but the pelvic-fin insertion averages farther back than in typical *R. o. robustus* or in *R. o. lethoporus*, but farther forward than in *R. o. reliquus*. In this subspecies, the distance from base of caudal to pelvic-fin insertion, when stepped forward, extends to any point one full eye length behind, to slightly before, rarely to as much as one eye length before, tip of snout; in typical *R. o. robustus*, to any point one pupil length behind to more than an eye length before tip of snout (in populations in springs of the Diamond Valley drainage the position of the pelvic may be intermediate). In radiographs, the pelvic insertion (table 17) lies below the 14th to 16th, usually the 15th or 16th, vertebra in *R. o. oligoporus*; usually below the 14th to 15th in typical *R. o. robustus*; usually below the 15th and 16th in some populations in the Diamond Valley drainage; usually below the 16th or 17th in *R. o. reliquus*; and below the 15th in *R. o. lethoporus*.

SEXUAL DIMORPHISM AND NUPTIAL CHARACTERS. Sexual dimorphism in the size of the fins (table 14) seems to be about average (the excessively large difference in the size of the caudal fin and the similar values for the sexes in the position of the dorsal fin in the fish from Location R10 seem attributable to the very small sample of adults).

The nuptial tuberculation agrees with the account given under the species heading (p. 98).

FIN RAYS (table 15). The counts of dorsal and anal rays are usually 8 and 7, respectively, as is characteristic of *Rhinichthys osculus* in general, but the rays in the paired fins are somewhat reduced in average number: this subspecies and *R. o. lethoporus* are the only ones among those under consideration that seem to have 6 pelvic rays oftener than 8, and these two and *R. o. reliquus*, and the set of three specimens of *R. o. robustus* from Carico Lake Valley, are the only ones that have 12 pectoral rays oftener than 14 or 15. The principal caudal rays are normally 19, of course, but many vary more than usual, from 18 to 21.

VERTEBRAE (table 16). The total vertebral counts are about as usual, but the precaudals seem to average slightly higher and the caudals slightly lower than usual.

SCALE ROWS. The four sets of scale counts (table 18) average definitely lower than in *R. o. reliquus*, about the same or not quite so low as in *R. o. lethoporus*, and somewhat lower than in *R. o. robustus* (except for some of the counts of the isolated populations of the Diamond Valley drainage system).

GILL-RAKERS. The rakers (table 18) at Location R11 seem to average very slightly lower than in other forms, but at Location R10 on the high side.

PHARYNGEAL TEETH. The 15 specimens examined for dentition yielded more than usual variation: 13 have the typical formula 1, 4—4, 1, but one each has 0, 4—4, 1; 1, 4—4, 0; and 1, 5—4, 1. The two listed as having no tooth in the lesser row of one side show no trace of an alveolus there. The count of 5 teeth on the main row of the left side of one apparently quite normal specimen, is, so far as we know, the only record of 5 for the entire genus. More than usual variability is suggested.

SEXUAL DIFFERENCES IN NUMBERS AND BIOMASS (tables 19, 20). The depleted populations of *R. o. oligoporus* sampled contained few adults. The two collections from Location R10, taken in August and September, contained 189 young 14 to 30 mm. in standard length, 3 adult males 40 to 41 mm. long, and 4 adult females 51 to 55 mm. long. Assuming that the unsexed young were equally divided by sex in numbers and size, the sex ratio is essentially equal, and the volumes are 18.5 ml. for males and 28.5 ml. for females, a ratio of 0.65:1.

The two collections from Location R11, also taken in August and September, contained 90 young 12 to 28 mm. long, 12 adult males 28 to 44 mm. long, and 16 adult females 28 to 59 mm. long. Assuming that the unsexed young were equally divided by sex in numbers and size, the sex ratio is 93 males to 100 females, and the volumes are 17.6 ml. for males and 43.9 ml. for females, a ratio of 0.40:1.

DERIVATION OF NAME. The name *oligoporus* was derived from ὀλίγος, few, and πορος, a passage through the skin. It is regarded as in the adjectival form.

INDEPENDENCE VALLEY SPECKLED DACE

Rhinichthys osculus lethoporus Hubbs and Miller.

(Figure 24C,D.)

Rhinichthys osculus lethoporus HUBBS and MILLER, 1972, p. 105 (diagnosis).

This subspecies, along with *Gila bicolor isolata* (p. 32, fig. 12), is confined to Warm Springs, the single spring complex in the entire expanse of Independence Valley (part of the basin of pluvial Lake Clover), in east-central Elko County, Nevada. These springs were mapped and briefly described, as "Ralph's Warm Springs," by Eakin and Maxey (1951b). The very limited other waters in the valley were definitely indicated by field reconnaissance to be fishless (pp. 31–32). The hydrographic and speciational relationship of this subspecies to the other subspecies occupying the basin of pluvial Lake Clover are discussed above under the heading of that form, *R. o. oligoporus*.

Location R12 (and G11).—Warm Springs of **Independence Valley**, a spring complex on the west margin of the north arm of the valley, just off the base of Pequop Mountains, approximately on the edge of the bed of pluvial Lake Clover, just below the 5,700-foot (1,737-m.) contour (on Elko 1:250,000 map), on either side of the T. 35–36 line near middle of R. 66 E., in east-central Elko County, Nevada (fig. 12). Water very clear, but easily muddied; thick clay-mud, firm in places; dense vegetation over bottom, very largely *Chara*, with some *Myriophyllum*, *Ceratophyllum*, a broad-leaved *Potamogeton*, and a sparse green alga; 26° C. (air 27°). Miller and Hubbs, August 25, 1965 (M65–33); UMMZ 186519 and 186905 (101, 18–39 mm.); 12-foot woven-mesh seine and 15-foot seine with ¼-inch square mesh.

An old reservoir, about 80 m. in diameter, presumably dating from when the abandoned cabins were occupied, receives most of the spring water, and a smaller pond was seen in the extensive grassy meadow below. A moist meadow extends to elevations at least 5 m. above the present level of the reservoir. The southernmost spring, 1.6 km. by road south of the ranch houses, we found to be an open, bubbling spring hole of warm water (30° C.). Here and in open, shallow sloughs bullfrogs, but no fish, were seen.

The tui chub, *Gila bicolor*, also occurs in the main spring, and is also represented by an endemic, somewhat dwarfed subspecies, *G. b. isolata* (pp. 175–180). The tui chubs abounded, but the speckled dace, in contrast, appeared to be so scarce, and so secretive, that it proved difficult to collect a good series. Not one specimen of *Rhinichthys* was included in the second collection. The

numbers of speckled dace are apparently being held down by introduced animals, especially largemouth bass, *Micropterus salmoides* (1 adult caught). An adult carp, *Cyprinus carpio*, was seen, and bullfrogs, *Rana catesbeiana*, were common. In 1966 Stephen H. Berwick (class report, University of California, Berkeley, 1966) found *Micropterus salmoides* present, was told by a ranch worker that carp occur, was informed by William Nisbet, a state fishery biologist, that exotic fish were probably not present in 1960, and that the bullfrogs, which abounded in 1966, were stocked by the state Department of Fish and Game about 10 years previously.

Despite the abundance of water (the main outflow was estimated by us to be about 200–300 gallons per minute), the local form of dace seems to be in the endangered category.

The circumstance that largemouth bass and carp occur in Warm Springs led us to wonder whether the dace and the chub might have been introduced. However, the state authorities, when checked for us by Donald E. Lewis, then Manager of the Ruby Lake National Wildlife Refuge, could provide no evidence of such stocking. Later, Thomas J. Trelease, Chief of Fisheries in the Nevada Fish and Game Department, indicated to us that he could find no record that the minnows had been introduced. Distinctive characters also lead to the conclusion that both species are native.

Description and Comparisons.

Holotype, UMMZ 186905, an adult female 35.3 mm. in standard length (fig. 24D). Paratypes, UMMZ 186519, all other known specimens (100, 18–39 mm. long), including the adult male, 34.1 mm. long, that is illustrated (fig. 24C). All specimens are from the same Location, R12 (data given above).

Next to *R. o. reliquus* (pp. 121–128), this is the most distinctive of the various local forms that appear from physiographic and systematic evidence to have been derived from *Rhinichthys osculus robustus*, or from its immediate ancestor.

In the following description, *R. o. lethoporus* is compared primarily with *R. o. oligoporus*, which occurs in the same pluvial lake basin.

Size. This appears to be the most dwarfed among all the local forms of *Rhinichthys* from springs in the area under consideration. The largest specimens among the 101 collected measure 34 mm. for males and 39 mm. for females, in standard length. The adults are not much larger than young of the year of some of the other forms. In degree of dwarfing, this form is closely approached only by the four warm-spring populations of the Lake Diamond drainage basin referred to *R. o. robustus* (table 20).

Coloration (fig. 24C,D). The general coloration is rather similar to that of *R. o. oligoporus*. The primary band is rather sharp, at least posteriorly, and a considerable trace of the lower lateral band is evident on most of the specimens. The dark speckling is usually very fine and tends to extend downward across the caudal peduncle (in this respect contrasting with *R. o. oligoporus* from Location R11, but not so strongly with those from R10). Many of the specimens show a blackish wedge or streak along the lower edge of the caudal peduncle. In contrast with *R. o. oligoporus*, at least a trace of a dark horizontal stripe, restricted largely to snout and upper part of opercle, is usually developed on the head, much as in *R. o. robustus*. In the blackening of the crotches of the bifurcating branches of the rays in the dorsal and caudal fins, and occasionally the anal fin, this subspecies resembles *R. o. robustus* more than *R. o. oligoporus*. Only a few of the preserved specimens show a light streak above the main lateral band (frequently shown by *R. o. oligoporus*). In general, the color pattern agrees with that of the other forms. The black wedge on the middle of the base of the caudal fin is occasionally conspicuous, as it usually is in *R. o. robustus*, but is commonly obsolescent, as in *R. o. oligoporus*. In the fine speckling of the lower sides, as well as in the form of the body, this form of *Rhinichthys* somewhat simulates the young of *Gila bicolor*.

Life colors. No bright colors were observed in the field.

Form (fig. 24C,D). The form of this subspecies, unusually compressed for a *Rhinichthys*, is particularly distinctive: the greatest width of the body steps about 2.0 times into the depth over the curve of the sides, rather than about 1.5 times as in *R. o. robustus* (in this respect *R. o. oligoporus* is approximately intermediate). The anterior profile is less flattened than in *R. o. robustus* and is less arched than in *R. o. oligoporus*. The anterior part of the head is more foreshortened than in *R. o. robustus*, but is rather more pointed (less rounded) than in *R. o. oligoporus*. The mouth is definitely straighter than in *R. o. oligoporus* and more oblique, rising forward to a horizontal through the lower edge of the eye.

Frenum. Not one of the specimens was observed to have a frenum.

Barbel (table 11). This subspecies is one of the three under consideration that almost invariably lacks the barbel. Among 79 specimens only 4 had a barbel on one side (minute in 3, small in 1), and none had a barbel on both sides.

Lateral-line system (table 12; figs. 25, 26). This form again, as are *R. o. reliquus* and *R. o. oligoporus*, is characterized by a great reduction in the development of the lateral line on the body, even more than in *R. o. oligoporus*, less extreme than in *R. o. reliquus*. An average pore count of 1.0 is not attained until the standard length reaches about 32 mm. and only 1 count higher than 6 was obtained among 136 sides enumerated.

The lateral-line system is also degenerate on the head. All 21 specimens examined for this character had the supratemporal canal interrupted. In this respect, the agreement is best with *R. o. reliquus* and contrasts somewhat with *R. o. oligoporus*. In some specimens even the lateral pores of this canal are represented merely by neuromasts.

Scale structure. The scales show the typical structure of *Rhinichthys* (p. 97).

Morphometry (table 13). In correlation with its compressed form, as noted above, the body proper, and more strikingly the caudal peduncle, are on the average deeper in each sex than in the other forms here treated. The relatively long head and the particularly large eye reflect the dwarfing of this form. The other head measurements are not particularly distinctive. As usual in *R. o. robustus* and its derivatives, the fins are small and rounded. On the average, the dorsal and anal fins are inserted farther back than in *R. o. robustus*, except for some of the populations isolated in the Diamond Valley drainage system; as far back, or farther, than in *R. o. oligoporus*. As determined from radiographs, the pelvic insertion lies under the 15th vertebra, occasionally under the 14th or 16th, less far back than in *R. o. reliquus* (table 17).

Particularly striking is the strong obliquity of the nearly straight mouth, so that the upper jaw rises to about the level of the middle of the eye. In *R. o. oligoporus* the mouth is more curved, and rises only to opposite the lower part of the eye. The difference in the angulation of the mouth is less striking in the young, which in all the subspecies of *Rhinichthys osculus*, and in many cyprinoid fishes, tend to have an oblique mouth, in correlation, presumably, with particulate midwater feeding on small invertebrates—a frequent developmental phenomenon, even of the white sucker, *Catostomus commersonnii* (Lacépède), as shown by Stewart (1926). This feature of *R. o. lethoporus*, therefore, appears to be a trophic adaptation in which the juvenile character is retained by the adult. In the bottomland Warm Springs of Independence Valley, where there has been considerable depth of relatively quiet, vegetated water, there would have been some advantage to midwater feeding throughout life, whereas in the shallow current on the alluvial slopes of the Clover Valley springs, inhabited by *R. o. oligoporus*, bottom feeding would have been more in order.

Sexual dimorphism and nuptial characters. Sexual dimorphism in the size of the fins (table 14) is relatively slight for the caudal and

TABLE 15. *Number of fin rays in populations of* Rhinichthys osculus *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality	Dorsal rays[1]				Anal rays[1]				
	7	8	9	Mean	5	6	7	8	Mean
Rhinichthys osculus robustus									
L. Lahontan (Humboldt R.)									
Carico L. Valley	—	3	—	8.0?	—	—	3	—	7.0?
Crescent Valley	4	30	—	7.88	—	—	34	—	7.00
Bishop Creek	2	74	—	7.97	—	1	74	1	7.00
Springs near Town Cr.	6	98	2	7.96	1	5	100	—	6.93
L. Franklin (introduced)									
Ruby Valley	1	13	—	7.93	—	1	13	—	6.93
L. Diamond									
Potts Ranch	—	52	—	8.00	—	1	56	—	6.98
Dianas Punch Bowl	4	90	6	8.02	—	2	92	6	7.04
Coils Creek	9	31	—	7.77	—	1	38	1	7.00
Birch Ranch	5	30	—	7.86	—	1	34	—	6.97
Big Shipley Spr.	8	28	—	7.78	1	4	30	1	6.86
Rhinichthys osculus reliquus									
L. Gilbert									
Grass Valley	2	77	10	8.09	—	5	74	9	7.05
Rhinichthys osculus oligoporus									
L. Clover									
9.5 mi. S. of Wells	11	31	1	7.77	—	2	40	1	6.98
Warm Sprs., Clover V.	3	38	—	7.93	—	1	39	1	7.00
Rhinichthys osculus lethoporus									
L. Clover									
Independence Valley	7	85	1	7.94	—	5	88	—	6.95

Subspecies / Pluvial lake system / Locality	Caudal rays[2]						Pelvic rays[3]					
	17	18	19	20	21	Mean	5	6	7	8	9	Mean
Rhinichthys osculus robustus												
L. Lahontan (Humboldt R.)												
Carico L. Valley	—	—	1	—	1	20.0?	—	—	1	5	—	7.8?
Crescent Valley	—	5	27	—	—	18.84	—	—	7	59	2	7.97
Bishop Creek	—	3	32	2	—	18.97	—	—	18	130	—	7.88
Springs near Town Cr.	—	8	22	1	1	18.70[4]	—	—	67	145	—	7.68
L. Franklin (introduced)												
Ruby Valley	—	1	13	—	—	18.93	—	—	22	32	—	7.59
L. Diamond												
Potts Ranch	—	—	30	—	—	19.00	—	—	39	83	—	7.68
Dianas Punch Bowl	2	11	85	1	—	18.83[5]	—	2	72	124	9	7.63
Coils Creek	—	5	34	1	—	18.90	—	3	71	281	2	7.79
Birch Ranch	1	—	27	2	—	19.00	—	—	129	37	—	7.22
Big Shipley Spr.	—	2	29	2	—	19.00	1	—	123	39	—	7.23
Rhinichthys osculus reliquus												
L. Gilbert												
Grass Valley	2	5	54	9	—	19.00	—	3	141	36	—	7.18
Rhinichthys osculus oligoporus												
L. Clover												
9.5 mi. S. of Wells	—	3	36	2	2	19 07	—	7	64	3	—	6.95
Warm Sprs., Clover V.	—	3	33	4	1	19.07	—	6	86	2	—	6.96
Rhinichthys osculus lethoporus												
L. Clover												
Independence Valley	—	3	28	1	—	18.94	—	9	103	6	—	6.97

[1] Last 2 elements counted as one ray.
[2] Principal rays: branched rays + 2.
[3] Both sides counted in most specimens.
[4] One count of 14 in an apparently normal, uninjured fin; included in calculation of mean.
[5] One count of 16 in an apparently normal, uninjured fin; included in calculation of mean.

(Table continued on next page.)

TABLE 15. CONTINUED.

Subspecies / Pluvial lake system / Locality	Pectoral rays[3]								
	9	10	11	12	13	14	15	16	Mean
Rhinichthys osculus robustus									
L. Lahontan (Humboldt R.)									
Carico L. Valley	—	—	—	4	2	—	—	—	12.3?
Crescent Valley	—	—	—	3	21	28	16	—	13.84
Bishop Creek	—	—	—	3	20	33	14	—	13.83
Springs near Town Cr.	—	—	—	7	31	52	8	1	13.65
L. Franklin (introduced)									
Ruby Valley	—	—	—	–	10	12	5	1	13.89
L. Diamond									
Potts Ranch	—	—	—	7	45	31	3	—	13.35
Dianas Punch Bowl	—	—	—	9	82	78	29	2	13.67
Coils Creek	—	—	—	7	24	40	9	—	13.64
Birch Ranch	—	—	—	13	30	19	8	—	13.31
Big Shipley Spr.	—	—	—	11	31	23	4	—	13.29
Rhinichthys osculus reliquus									
L. Gilbert									
Grass Valley	—	—	6	53	65	15	—	—	12.65
Rhinichthys osculus oligoporus									
L. Clover									
9.5 mi. S. of Wells	—	—	4	16	21	2	—	—	12.49
Warm Sprs., Clover V.	1	—	—	19	31	7	—	—	12.72
Rhinichthys osculus lethoporus									
L. Clover									
Independence Valley	—	1	1	16	35	5	—	—	12.72

TABLE 16. *Number of vertebrae in populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Subspecies / Pluvial lake system / Locality	Precaudal						Caudal[2]						Total[2]						
	18	19	20	21	22	Mean	16	17	18	19	20	Mean	35	36	37	38	39	40	Mean
R. o. robustus																			
L. Lahontan (Humboldt R.)																			
Carico L. Valley	—	—	2	1	—	20.3?	—	—	2	—	—	18.0?	—	—	—	1	1	—	38.5?
Crescent Valley	—	9	18	2	—	19.76	—	2	21	6	—	18.14	—	—	6	20	3	—	37.90
Bishop Creek	5	12	—	—	—	18.71	—	2	12	3	—	18.06	—	6	11	1	—	—	36.72
Springs near Town Cr.	—	12	7	—	—	19.35	—	1	8	4	—	18.23	—	—	7	5	1	—	37.54
L. Franklin (introduced)																			
Ruby Valley	—	5	5	1	—	19.64	—	—	4	5	—	18.55	—	—	1	5	3	—	38.22
L. Diamond																			
Potts Ranch	2	10	7	—	—	19.26	1	12	4	—	—	17.18	—	7	10	—	—	—	36.59
Dianas Punch Bowl	6	8	6	—	—	19.00	—	2	11	5	2	18.35	—	2	10	4	4	—	37.50
Coils Creek	—	4	13	2	—	19.85	—	7	9	—	—	17.44	—	—	9	6	1	—	37.50
Birch Ranch	4	18	11	—	1	19.29	—	14	15	2	—	17.61	—	8	17	5	—	1	37.00
Big Shipley Spr.	—	10	10	1	—	19.56	—	5	13	1	—	17.84	—	1	9	9	—	—	37.42
R. o. reliquus																			
L. Gilbert																			
Grass Valley	—	11	16	10	—	19.97	21	13	3	—	—	16.51	3	16	15	3	—	—	36.49
R. o. oligoporus																			
L. Clover																			
9.5 mi. S. of Wells	—	2	18	12	—	20.31	12	18	2	—	—	16.69	—	4	24	4	—	—	37.00
Warm Sprs., Clover V.	—	4	12	5	—	20.05	2	10	5	2	—	17.37	—	3	6	8	3	—	37.55
R. o. lethoporus																			
L. Clover																			
Independence Valley	1	9	10	—	—	19.45	1	11	5	—	—	17.24	—	7	11	1	—	—	36.68

[1] All counts from radiographs.
[2] Including hypural complex (as 1) and the 4 vertebrae comprising the Weberian apparatus.

TABLE 17. *Position of pelvic-fin insertion, in terms of overlying vertebra, in populations of* Rhinichthys osculus *in certain basins in Nevada.*

Subspecies Pluvial lake system Locality	Vertebra no. (from radiographs) 13	14	15	16	17	18	Mean
Rhinichthys osculus robustus							
L. Lahontan (Humboldt R.)							
Carico L. Valley	—	—	1	2	—	—	15.7?
Crescent Valley	—	1	17	14	1	—	15.45
Bishop Creek	1	3	12	1	—	—	14.76
Springs near Town Cr.	4	9	6	—	—	—	14.11
L. Franklin (introduced)							
Ruby Valley	—	2	6	3	—	—	15.09
L. Diamond							
Potts Ranch	1	7	10	2	—	—	14.65
Dianas Punch Bowl	—	6	7	7	—	—	15.05
Coils Creek	—	—	12	8	—	—	15.40
Birch Ranch	2	8	11	—	—	—	14.43
Big Shipley Spr.	1	3	10	6	—	—	15.05
Rhinichthys osculus reliquus							
L. Gilbert							
Grass Valley	—	—	2	21	15	1	16.38
Rhinichthys osculus oligoporus							
L. Clover							
9.5 mi. S. of Wells	—	1	11	7	—	—	15.32
Warm Sprs., Clover V.	—	2	12	11	—	—	15.36
Rhinichthys osculus lethoporus							
L. Clover							
Independence Valley	—	3	16	3	—	—	15.00

TABLE 18. *Number of scale rows and gill-rakers in populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Subspecies Pluvial lake system Locality	Scale rows: Lateral-line series	Predorsal series	Around body	Around peduncle	Gill-rakers (total)
R. o. robustus					
L. Lahontan (Humboldt R.)					
Carico L. Valley	69–78(73.7_{3})	38–43(40.0_{3})	59–64(61.7_{3})	30–34(31.7_{3})	6–8 ($7.0?_{3}$)
Crescent Valley	66–75(70.5_{20})	40–47(42.9_{20})	52–72(66.8_{20})	32–40(35.9_{20})	6–10(7.30_{20})
Bishop Creek	59–70(63.8_{20})	35–41(38.3_{18})	57–68(61.8_{16})	30–33(31.3_{17})	5–9 (7.30_{20})
Springs near Town Cr.	62–70(66.8_{20})	33–46(40.7_{19})	58–70(64.7_{20})	28–34(32.2_{19})	6–9 (7.35_{20})
L. Franklin (introduced)					
Ruby Valley	61–69(64.9_{11})	33–43(38.9_{14})	60–66(63.7_{11})	32–36(33.4_{11})	6–9 (7.47_{15})
L. Diamond					
Potts Ranch	54–64(59.3_{20})	33–41(35.8_{20})	56–67(61.4_{11})	30–34(32.1_{16})	6–9 (7.41_{22})
Dianas Punch Bowl	56–72(61.8_{13})	31–44(36.8_{13})	54–69(59.3_{13})	29–33(30.6_{13})	6–9 (7.50_{20})
Coils Creek	58–72(65.5_{19})	37–44(40.3_{19})	60–70(64.4_{10})	31–34(32.3_{10})	5–10(8.05_{19})
Birch Ranch	52–65(57.9_{23})	32–40(34.7_{23})	55–62(58.7_{20})	28–32(30.7_{21})	6–10(7.33_{27})
Big Shipley Spr.	52–71(58.7_{16})	32–38(34.8_{20})	53–60(55.7_{15})	28–32(29.7_{16})	7–10(7.65_{20})
R. o. reliquus					
L. Gilbert					
Grass Valley	60–74(66.4_{30})	37–47(41.6_{27})	56–76(66.5_{22})	32–40(36.2_{27})	6–9 (7.21_{34})
R. o. oligoporus					
L. Clover					
9.5 mi. S. of Wells	54–60(57.5_{6})	35–38(36.7_{6})	58–62(59.8_{5})	29–32(30.2_{6})	7–9 (8.00_{6})
Warm Sprs., Clover V.	54–66(59.3_{17})	34–40(37.3_{15})	52–60(55.5_{15})	28–31(29.9_{10})	5–9 (7.07_{15})
R. o. lethoporus					
L. Clover					
Independence Valley	50–62(56.3_{21})	26–35(29.8_{21})	48–60(53.5_{21})	26–34(29.7_{20})	6–10(7.90_{20})

[1] For each entry there is given the observed range and, in parentheses, the mean, with the number of specimens as a subscript.

TABLE 19. *Sex ratios by number and by biomass for populations of* Rhinichthys osculus *in certain basins in Nevada.*[1]

Subspecies / Pluvial lake system / Locality	Sex ratio by M per 100 F	Sex ratio by Biomass, M/F
R. o. robustus		
L. Lahontan (Humboldt R.)		
Crescent Valley	47	.30
Bishop Creek	67	.48
Springs near Town Cr.	54	.38
L. Franklin (introduced)		
Ruby Valley	75	.26
L. Diamond		
Potts Ranch	124	1.10
Dianas Punch Bowl	80	.69
Coils Creek	52	.36
Birch Ranch	96	.63
Big Shipley Spr.	25	.12
R. o. reliquus		
Lake Gilbert		
Grass Valley	63	.27
R. o. oligoporus		
Lake Clover		
9.5 mi. S. of Wells	75?	.65
Warm Sprs., Clover Valley	93	.40
R. o. lethoporus		
Lake Clover		
Independence V.	80	.65

[1] Based on detailed data in table 20

the pelvic, about medium for the dorsal, among the highest for the pectoral (averaging 5.2 percent of the standard length longer in males than in females). This high dimorphism in the size of the pectoral fin indicates that we are dealing with dwarfed adults, not merely with young specimens, and confirms that we are describing a distinct form. The single August 25 collection has not provided specimens in nuptial condition. The sexes differed little in size (see below).

MERISTICS (tables 15, 16, 18). Dorsal rays usually 8, occasionally 7, very rarely 9; anal 7, occasionally 6. The pectoral rays, as in subspecies *R. o. reliquus* and *R. o. oligoporus*, average few (12.72 for 58 counts). The pelvic-ray counts, 7, with variants of 6 seemingly exceeding those of 8, also yield a low average. The principal caudal rays are typically 19, but vary from 18 to 20. The vertebral counts average 19.45 precaudal, 17.24 caudal, and 36.68 total, slightly fewer than in *R. o. oligoporus*. The scale counts, averaging 56.3 in lateral-line series, 29.8 in predorsal rows, 53.5 around body, and 29.7 around peduncle, are usually fewer than in any of the other forms under treatment (table 18). The trend toward low ray counts seems to be related to the dwarfing of this form. The gill-raker counts, however, average slightly on the high side (table 18).

PHARYNGEAL TEETH. The 5 specimens counted have the expected tooth formula, 1, 4—4, 1. The single tooth of the lesser row is strong.

SEXUAL DIFFERENCES IN NUMBERS AND BIOMASS (tables 19, 20). This form is greatly dwarfed, to the extent that it has been apparently impossible to separate young from adults by size. Collecting in the very dense vegetation was so difficult that some young probably escaped, although the fish were taken by a fine-meshed woven ("Common Sense") seine, as well as by a tied-mesh seine, and special effort was expended to secure a representative sample. The compressed grouping, with males predominating in the lower size groups, suggests that at most only a few of the larger young were seined. All specimens were sexed by gonad examination. The 101 specimens that we were able to collect comprised 45 males 18–34 mm. in standard length, mostly in the 2.5-mm. and 3.0-mm. size groups, and 56 females 21–39 mm. long, mostly in the 2.5-mm. to 3.5-mm. size groups. The average standard lengths of the sexes were extremely close, 26.7 and 30.1 mm., for the males and females, respectively. The sex ratio, 80 males to 100 females, is much closer to equality than in the other populations, as is also the ratio of males to females by bulk, .65:1. The close similarities between the sexes in numbers, mass, and size presumably reflect the extreme dwarfing, and suggest that this subspecies may be an annual fish.

DERIVATION OF NAME. The name *lethoporus* was derived, figuratively, from λήθη, a forgetting, and πόρος, a passage through the skin. It is regarded as in adjectival form.

TABLE 20. *Size frequency and biomass for all specimens, by sex, for all populations sampled of* Rhinichthys osculus *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality	Date of coll.	N, Sex	S.L., mm.	Biomass, ml.	Number of specimens per 0.5-cm size groups: 1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0
R. o. robustus																					
L. Lahontan (Humboldt R.)																					
Carico L. Valley	V:25	3♀	57–64	10.6	—	—	—	—	—	-	—	—	—	1	1	1	—	—	—	—	—
Crescent Valley	VIII:10	9♂♀	13–20	0.4	—	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		49♂	32–64	138.0	—	—	—	—	1	—	—	6	13	23	5	1	—	—	—	—	—
		104♀	35–88	460.0	—	—	—	—	—	1	1	13	13	10	27	21	9	5	3	—	1
Bishop Creek	VI:29	1♂♀	18	0.1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		31♂	29–45	24.1	—	—	—	—	7	17	2	5	—	—	—	—	—	—	—	—	—
		46♀	26–60	50.5	—	—	—	2	16	13	4	3	3	2	3	—	—	—	—	—	—
Springs near Town Cr.[1]	VI:29	42♂♀	15–21	4.4	—	9	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		43♂	31–47	36.7	—	—	—	—	4	25	9	5	—	—	—	—	—	—	—	—	—
		79♀	30–59	97.4	—	—	—	—	3	37	21	8	6	2	2	—	—	—	—	—	—
L. Franklin (introduced)																					
Ruby Valley	VIII:8	4♂♀	14–21	0.5	—	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12♂	23–41	8.8	—	—	—	4	4	—	4	—	—	—	—	—	—	—	—	—	—
		16♀	23–74	34.0	—	—	—	3	3	—	1	2	4	2	—	—	—	1	—	—	—
L. Diamond																					
Potts Ranch	VIII:16	57♂	19–37	37.2	—	—	4	11	23	19	—	—	—	—	—	—	—	—	—	—	—
		46♀	22–46	33.9	—	—	2	8	14	13	6	3	—	—	—	—	—	—	—	—	—
Dianas Punch Bowl	II:9,19	86♂	22–38	54.5	—	—	3	16	33	32	2	—	—	—	—	—	—	—	—	—	—
		107♀	21–48	85.7	—	—	1	19	29	41	11	5	1	—	—	—	—	—	—	—	—
Coils Creek	VIII:15	579♂♀	13–27	85	—	36	427	116	—	—	—	—	—	—	—	—	—	—	—	—	—
		191♂	32–52	234	—	—	—	—	2	54	78	46	11	—	—	—	—	—	—	—	—
		366♀	34–71	642	—	—	—	—	1	67	151	60	32	33	14	4	4	—	—	—	—
Birch Ranch	VIII:13	6♂♀	17–20	—	—	1	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		89♂	22–41	51.2	—	—	1	28	32	19	9	—	—	—	—	—	—	—	—	—	—
		93♀	20–65	81.0	—	—	7	35	20	9	6	11	3	1	—	1	—	—	—	—	—
Big Shipley Spr.	VIII:13	82♂	23–37	47	—	—	—	23	39	20	—	—	—	—	—	—	—	—	—	—	—
		333♀	22–55	384	—	—	2	33	73	76	82	44	21	2	—	—	—	—	—	—	—
R. o. reliquus																					
L. Gilbert																					
Grass Valley	VIII:9	183♂	12–47	136	1	1	7	14	21	95	39	5	—	—	—	—	—	—	—	—	—
		291♀	17–82	498	—	2	14	12	4	70	84	44	18	6	13	10	6	7	1	—	—
R. o. oligoporus																					
L. Clover																					
9.5 mi. S. of Wells	VIII:26 and IX:14	189♂♀	14–30	29.7	—	42	115	27	5	—	—	—	—	—	—	—	—	—	—	—	—
		3♂	40–41	3.6	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—
		4♀	51–55	13.6	—	—	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—
Warm Springs, Clover V.	VIII:26 and IX:14	90♂♀	12–28	13.0	1	28	35	25	1	—	—	—	—	—	—	—	—	—	—	—	—
		12♂	28–44	12.1	—	—	—	—	1	1	8	2	—	—	—	—	—	—	—	—	—
		16♀	28–59	37.4	—	—	—	—	1	1	1	2	5	5	1	—	—	—	—	—	—
R. o. lethoporus																					
L. Clover																					
Independence Valley	VIII:25	45♂	18–34	20.2	—	—	7	18	19	1	—	—	—	—	—	—	—	—	—	—	—
		56♀	21–39	31.1	—	—	2	14	24	13	3	—	—	—	—	—	—	—	—	—	—

[1] Many young were discarded in the field.

TUI CHUB

Gila bicolor (Girard).

Under this species name we treat all native chubs that occur in the area of Nevada under report (pp. 1–2), along with the two common forms, '*pectinifer*' and '*obesa*,' of the central part of the Lake Lahontan system. Different types from disjunct basins are referred to several distinct subspecies (table 21). In view of the complicated interrelationships of these forms, and their confused classification and nomenclature, some consideration needs first to be given to the Lahontan forms. Although we have long had other related forms under study, we refrain in this report from treating the several unnamed subspecies that we have indicated (Hubbs and Miller, 1948b, p. 91) as occurring in different springs in the drainage basin of pluvial Lake Railroad, which lies within the area on which we are reporting, as well as various extralimital subspecies that occur in other endorheic basins in the drainages of pluvial lakes Toiyabe (*q. v.*), Dixie, and White Mountains in western Nevada, as well as various forms that occupy, or until recently occupied, lake basins in California, southeastern Oregon, and southeastern Washington (Hubbs and Miller, 1948b, pp. 43–45, 61–67, 70–74; Miller, 1973, pp. 1–8).

The populations of Railroad Valley have been referred by us (Hubbs and Miller, 1948b, p. 91) to *Siphateles obesus* and by Bradley and Deacon (1965, p. App. II-1) to *Gila bicolor*. A wide-ranging subspecies occurs in Little Fish Lake, in Twin Springs near the outlet end of Hot Springs Valley, and in the Duckwater Creek tributary to Railroad Valley (also in Artesian Well No. 7 in the playa of Railroad Valley, presumably as a result of floodwater incursion from either Twin Springs or Duckwater Creek). That form we have found to occur also, presumably as a result of stocking from Twin Springs, in Stone Cabin (or Willow Creek) Valley, just to the southwest, across a definite divide (p. 232).

General Appraisal Of Lahontan Subspecies

Several complications arise in the classification and nomenclature of the forms listed in table 21. The generic pertinence of the species calls for discussion first. Until very recently, the species complex involved has been treated under the generic name *Siphateles*. On the basis of Teruya Uyeno's doctoral study (1960), *Siphateles* has been synonymized with *Gila*. Preliminary notices to that effect have been given by Miller (1961, p. 384; 1968, p. 171) and by Bailey and Uyeno (1964), and the species name '*bicolor*' is listed under *Gila* by Bailey *et al.* (1960, p. 13; 1970, p. 20). The basis for this action has been (1) the indication of the very close agreement between "*Siphateles obesus*" (*Gila bicolor obesa*) and the Utah chub, *Gila atraria* (Girard) in external and, especially, in skeletal characters, and (2) the opinion that these points of agreement overbalance the difference in dentition that previously had been accorded greater weight. The

Table 21. *Local forms of* Gila bicolor *within the area of the present study and in the central part of the Lahontan system.*[1]

Subspecies	Pluvial lake system	Valley
Gila bicolor pectinifer (Snyder)	Lahontan	Humboldt R., etc.
Gila bicolor obesa (Girard)	Lahontan	Humboldt R., etc.
Gila bicolor obesa (2 aberrant stocks)	Diamond	Diamond
Gila bicolor newarkensis	Newark	Newark
Gila bicolor euchila	Newark	Fish Creek (Little Smoky)
Gila bicolor isolata	Clover	Independence
Gila bicolor: several unnamed subspecies, still under study	Railroad	Railroad; Warm Springs; Little Fish Lake

[1] The four subspecies other than *G. b. pectinifer* and those of the basin of Lake Railroad are listed in more detail on page 150 and are treated in detail in this report.

circumstance that the pharyngeal teeth of *Siphateles* are invariably uniserial, whereas in all species of *Gila* (*sensu stricto*) these teeth are biserial, was discounted, because the same difference frequently exists within other recognized genera and even within species, and the difference in dentition may have merely trophic implications. However, the whole problem of generic limitations in the Holarctic Cyprinidae is presently in almost utter confusion. We merely adopt for the present discussion what seems to be the current trend. The decision has little effect on the problems of the present report, except for the indication that the Lahontan and Bonneville species, respectively '*bicolor*' and '*atraria*,' are now believed to be much more intimately related than was signified by their generic separation.

Some of the osteological features of *Gila bicolor* are briefly indicated in the diagnosis of the genus *Relictus* (pp. 182–193).

SPECIES NAME. The specific name *bicolor* is accepted in place of *obesa* on the basis of a nomenclatural muddle that Bailey and Uyeno (1964) clarified. The name *obesa* remains available, and has been accepted, for a Lahontan subspecies.

STATUS OF THE LACUSTRINE TYPE (*pectinifer*). Problems of taxonomy as well as nomenclature are involved in the treatment of '*pectinifer*' as well as '*obesa*' as subspecies of *Gila bicolor*. In describing *Leucidius pectinifer*, Snyder (1917, pp. 60–67, figs. 4–6) distinguished this form as a distinct genus on the basis of its very numerous gill-rakers, 29 to 36 and its tooth formula, 5—5 *vs.* 5—4. However, as we note in the discussion (pp. 146–149) of the gill-raker character, there is a complete gradation between topotypic '*obesa*,' with 11 to 19 rakers, and '*pectinifer*,' with counts to 40. Furthermore, isolated populations show all levels of raker number, as we have shown in studies hopefully leading toward a revision of the whole group. Some specimens of '*pectinifer*' have 5—4 teeth and some of '*obesa*' have 5—5 teeth. The proportion of specimens of the '*obesa*' type with 5—5 teeth is highest in series, like that from Carson River near Fallon and from the Humboldt River near Lovelock (table 23), that apparently show introgression from '*pectinifer*' also in the increased and skewed raker number (table 22).

The striking increase in raker number and length in '*pectinifer*' is paralleled again and again among cyprinids and other freshwater fishes, throughout the world, as they have assumed a lacustrine existence. The structural modification is clearly related to the well authenticated notable abundance of plankton in lakes and general paucity in streams. The less robust teeth of '*pectinifer*,' numbering 5—5, probably constitute a parallel adaptation.

Essentially, '*pectinifer*' and '*obesa*' appear to be trophic adaptations with, in general, ecological segregation (which has been decreasing, with the agriculture-based desiccation of the waters). As indicated in the discussion of the gill-raker character (pp. 146–149), the high number and greater length of the rakers in '*pectinifer*' is interpretable as an adaptation to plankton feeding in the lakes it inhabits, currently the remnant lakes of the Lahontan basin. We may assume that it abounded throughout Lake Lahontan, as Snyder (1917, p. 66) found it to swarm in Pyramid Lake, "approaching the shore at times in enormous schools," that "resemble large purple clouds." In Lake Lahontan it was presumably almost completely segregated from the fluviatile form (*obesa*).

After noting that *Leucidius pectinifer* had "been reduced to a subspecies of *S. bicolor*, of which it is considered to be the lacustrine form," La Rivers and Trelease (1952, p. 117) put forth the following proposition:

> However, on the basis of recent data, we are convinced that *pectinifer* has no valid standing as a taxonomic unit. Genetically, *pectinifer* might be preserved to indicate tui chub with fine gill rakers (as Shapovalov and Dill, 1950, have done), just as it might be feasible, under some circumstances, to so distinguish between people with blue eyes and people with brown eyes. Chub with coarse gill rakers occur side-by-

> side with individuals with fine gill rakers, contrary to Snyder's supposition that he could observe them segregating in separate schools in the lake. Gill net sampling in Pyramid Lake by the writers has resulted in catches of chubs with both types of gill rakers at the same time and place, and there is no sexual correlation between raker differences. Whether there are any differences in feeding habits between the two types remains to be seen, but the above sampling, during the winter, showed both to be mixed in the same schools and to be feeding on the bottom on the same materials. It is possible that at other times of the year one form may have an advantage over the other in being able to obtain more plankton from the water, but at present, that is a dubious point.

Later (1962, pp. 412–421, figs. 192, 193) La Rivers expanded on the same line, obviously not cognizant of the large stream populations of *G. bicolor obesa*. He still felt "convinced that *pectinifer* has no valid standing as a taxonomic unit."

We regard as wholly untenable the view that '*obesus*' and '*pectinifer*' should not be distinguished. That view was not supported by Shapovalov and Dill, who, on our recommendation, merely listed the two forms as subspecies of the tui chub, "*Siphateles*" *bicolor*. Snyder collected sizable series (he listed 81 counts of scales). He took '*pectinifer*' only in lakes and he did give some evidence (p. 67) of segregation. The two types differ not only in the number and length of the rakers, but also in dentition, body and head form, and usually in scale number. They do, however, intergrade, and probably have done so increasingly as surface waters have diminished through agricultural use.

For about three decades *Leucidius* has been treated as a synonym of *Siphateles* and by some authors *S. pectinifer* and *S. obesus* have been interpreted as only subspecifically distinct, primarily on the basis of apparent trophic adaptation and of extensive introgression and intergradation, with occasional fusion (Hubbs, 1941, p. 188; Hubbs and Miller, 1943, p. 352; 1948b, pp. 41–42; Shapovalov and Dill, 1950, p. 386). The essentially undocumented interpretation was somewhat elaborated later (Hubbs, 1961, pp. 13–14). Some further indication of introgression is furnished in the present report, and much further confirmatory data have been gathered by us in a survey of variation in *Siphateles* throughout its range.

Because of the tendency toward sympatry of the two types in certain large lakes, particularly Lake Tahoe, Richard G. Miller (doctoral thesis, Stanford University, 1951) and Hopkirk and Behnke (1966, p. 136) have, in strong contrast with the opinion of La Rivers, interpreted '*obesa*' and '*pectinifer*' as *specifically* distinct. However, our studies have provided evidence of wholesale introgression and hybridization wherever the two types have met. In Eagle Lake, California, fusion of the two types has apparently led to the origin of a taxon with a distinctly bimodal, intermediate number of rakers (Kimsey, 1954, pp. 397–398, fig. 2), though essentially uniform in the other taxonomic characters.

We strongly suspect that where both occur in a lake the two types are segregated by schools and by habitat. Snyder, as noted above, wrote of huge schools of '*pectinifer*' in Pyramid Lake, and we have studied in detail (Hubbs, 1961, pp. 13–14) a large collection from the inlet end of Walker Lake that was uniformly typical of '*pectinifer*' in all characters, except that a considerable proportion had, as an apparent result of introgression, the low raker number of '*obesa*,' and others had a dribbling range of counts fully connecting the high '*pectinifer*' and the low '*obesa*' modes.

Admittedly, the interplay between '*pectinifer*' and '*obesa*' could be interpreted as extensive interspecific hybridization rather than as subspecific intergradation. It is one of many cases in which the distinction is to a large degree arbitrary, such as one of us (Hubbs, 1943) indicated long ago. We favor the view that the extensive interchange in genes is better interpreted as intraspecific than as interspecific. Our reasoning parallels that advanced by us (Miller and Hubbs, 1969) for retaining the commoner of the widespread forms of the threespine stickleback as subspecies of a single species, *Gasterosteus aculeatus* Linnaeus.

TABLE 22. *Number of gill-rakers in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies Pluvial lake system Locality[1]	Gill-rakers, including all rudiments, on first gill-arch																	
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	No.	Ave.
Gila bicolor obesa																		
Lake Lahontan																		
Carson River (G1)[2]	—	—	—	—	1	6	9	13	13	8	5	5	5	1	3	1	70	16.43
Humboldt River																		
Near Lovelock (G2)	—	—	—	—	3	16	32	37	29	15	5	2	2	2	2	—	145	14.90
Near Carlin (G3)	—	—	—	2	5	23	16	13	—	1	—	—	—	—	—	—	60	13.62
Bishop Creek (G4)	—	—	1	16	66	83	25	1	—	—	—	—	—	—	—	—	192	12.61
Lake Diamond																		
Birch Ranch (G5)	—	—	—	—	9	28	22	9	2	—	—	—	—	—	—	—	70	13.53
Sulphur Spring (G6)	—	—	—	—	5	22	43	12	—	—	—	—	—	—	—	—	82	13.76
Gila bicolor newarkensis																		
Lake Newark																		
Near Diamond Peak (G7)	—	1	8	23	38	22	5	3	—	—	—	—	—	—	—	—	100	11.99
Moores Ranch (G8)	—	—	2	14	39	34	11	—	—	—	—	—	—	—	—	—	100	12.23
Warm Springs (G9)	—	—	—	2	6	—	—	—	—	—	—	—	—	—	—	—	8	11.75
Gila bicolor euchila																		
Lake Newark																		
Fish Creek Springs (G10)	—	—	13	40	56	24	5	—	—	—	—	—	—	—	—	—	138	11.77
Gila bicolor isolata																		
Lake Clover																		
Independence Valley (G11)	2	9	30	53	36	18	1	—	—	—	—	—	—	—	—	—	149	11.14

[1] Expressed as numbered Locations in the G series.
[2] Some introgression from *Gila bicolor pectinifer.*

One example of apparent introgression from *G. b. pectinifer* into *G. b. obesa* is furnished by our analysis of a sample of subtypical '*obesa*' from the lower reaches of Carson River, one of the areas in which we find the numbers of gill-rakers increased and markedly skewed in distribution (table 22). The same lot shows a somewhat increased proportion of specimens with the 5—5 dentition characteristic of '*pectinifer*' (see below, and table 23). Yet the very slight positive correlation between raker and tooth counts (table 24) seems to indicate essential integration of the stock, following some degree of long-past hybridization. In the apparently well integrated form of presumed hybrid origin, in Eagle Lake (mentioned above), the proportionate number of specimens with 5—5 teeth is about the same in the modal groups with rather few and rather many rakers: 5 among the 28 with 12–19 and 5 among the 33 with 23–30 rakers (data from J. B. Kimsey's A. M. thesis, University of California, Berkeley); apparently there is some genetic segregation in the inheritance of gill-raker number in *Gila bicolor*, as evidenced also by the case mentioned by Hubbs (1961, pp. 13–14).

The tooth and gill-raker counts throughout the Humboldt River system and in the basins disjunct therefrom provide almost no evidence of introgression from *G. b. pectinifer* in this area, except in so far as the upstream downward cline in gill-raker number (table 22) may be construed as such evidence. It is plausible to infer that the upper Humboldt River, from which, presumably, the isolated basins of pluvial lakes Diamond, Newark, and Clover originally received their *Gila bicolor* stocks, was populated during some Pleistocene time by *G. b. obesa* rather than by *G. b. pectinifer*. The circumstance that lacustrine types with a high number of rakers apparently did not evolve in any of these three ancient lakes suggests that such adaptation is not particularly rapid and/or inevitable. Of course, it is remotely possible, though seemingly improbable, that rakers did increase in number in the ancient lakes, but reverted (through reverse adaptation) to the low number after the fish had become limited to springs and

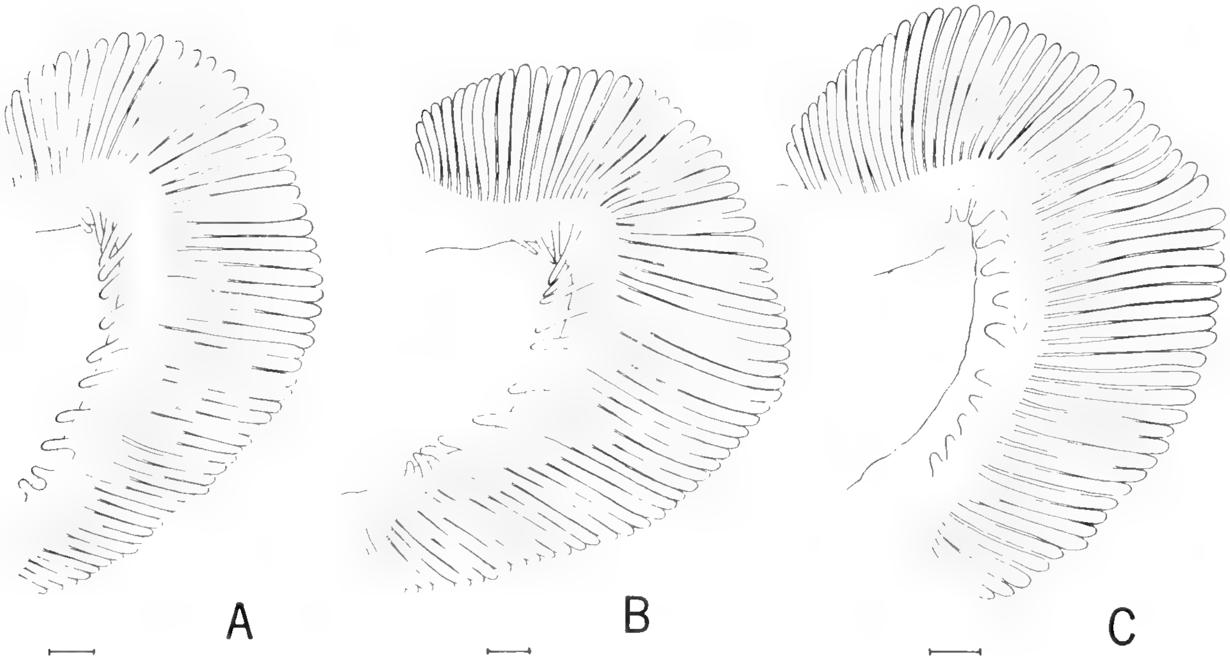


FIGURE 28. First gill-arches, with gill-rakers, in three races (two subspecies) of *Gila* (*Siphateles*) *bicolor* from separate basins in Nevada, based on adults of comparable size. Scales represent 1.0 mm. Drawn by Martha B. Lackey. A. *G. b. obesa*, considered topotypic: Humboldt River near Lovelock (Location G2); UMMZ 124873, no. 5; 90 mm. B. *G. b. obesa*, aberrant race: Sulphur Spring, Diamond Valley (G6); UMMZ 124928, no. 8; 88 mm. C. *G. b. newarkensis*, paratype: spring in Newark Valley near Diamond Peak (G7); UMMZ 132185, no. 8; 85 mm.

spring creeks. However, in the Mohave River system, a lacustrine type with many rakers, which we now treat as *Gila bicolor mohavensis* (Snyder), has persisted under postpluvial conditions that are conducive to fluviatile types (Hubbs and Miller, 1943). In the Lake Railroad system, similar types with moderately numerous rakers have persisted in isolated springs.

NUMBER AND LENGTH OF GILL-RAKERS. The degree of development of rakers determined by methods outlined on pages 92–93, and expressed by their total number and by their concordant length (tables 22, 25), provides some of the most significant indications of differentiation among the isolated stocks of *Gila* (*Siphateles*) *bicolor* in the basins under consideration. This was to be expected, since gill-raker development is closely correlated with size and type of available food and often differs markedly in different stocks, yet is widely recognized as being usually fixed genetically.

Within stocks, and more loosely between stocks, the number and the form of the rakers are correlated, so that the difference in appearance is accentuated. When very few, as in *G. b. newarkensis* (fig. 28C), the rakers are usually very thick, opaque and fleshy, nearly smooth, and nearly or quite in juxtaposition basally, whereas in topotypic *G. b. obesa* (fig. 28A) the rakers are rather slender, translucent and bony, moderately denticulate or crenulate on the inner edge, and generally well separated at the base. This contrast is particularly sharp between *G. b. newarkensis* and the Sulphur Spring race (fig. 28B) of *G. b. obesa*.

The number of rakers in *Gila bicolor* varies extraordinarily, from 8 to 40, without any hiatus, and with many modes represented among the multitude of local forms we have had under study, not only in the Humboldt River system and the once connected endorheic basins (table 1), but also generally in the isolated waters in central and

northern Nevada, central and eastern California, southeastern Oregon, and southeastern Washington. As explained above, some distinct and geographically separated forms have similar counts. The contrast between the subspecies is accentuated, for it involves also the length and crowding of the rakers—as was shown by Snyder (1917, figs. 4–5) in contrasting the rakers of the forms he called *Leucidius pectinifer* and *Siphateles obesus*. The example of '*obesus*' he figured shows about 22 rakers and presumably represents (1) hybrid origin; or (2) introgression from '*pectinifer*,' which occurred in the same lake (Winnemucca); or (3) an independent modification of *G. b. obesa* toward the lacustrine type. The two types both occur in some lakes with a complete range of intermediates, due apparently to hybridization and intergradation.

The marked differences in raker length, and correlated differences in their form, have been confirmed by casual examination of many more specimens than are entered in table 25. Such examination, for example, was accorded nearly all of the specimens, mostly of small size, that were utilized in enumerating the pharyngeal teeth (table 23).

Although a positive correlation exists in general in *Gila bicolor* between the length and the number of gill-rakers—particularly exemplified in contrasting typical populations of *G. b. obesa* and *G. b. pectinifer*—no sharp or regular correlation exists among the stocks treated in this report. The adaptations of increased number and increased length of rakers have apparently been to a large degree independent. The rather complex relations between the mean length of longest raker (table 25) and the mean numbers of rakers (table 22) become evident when these two parameters are plotted together (fig. 29). The samples (1–4) from the Humboldt River system (fig. 28A) have similar, median raker lengths, but decrease regularly in mean number from downstream to headwaters. In the two populations from Diamond Valley, regarded as variants of *G. b. obesa*, the rakers are alike in median number

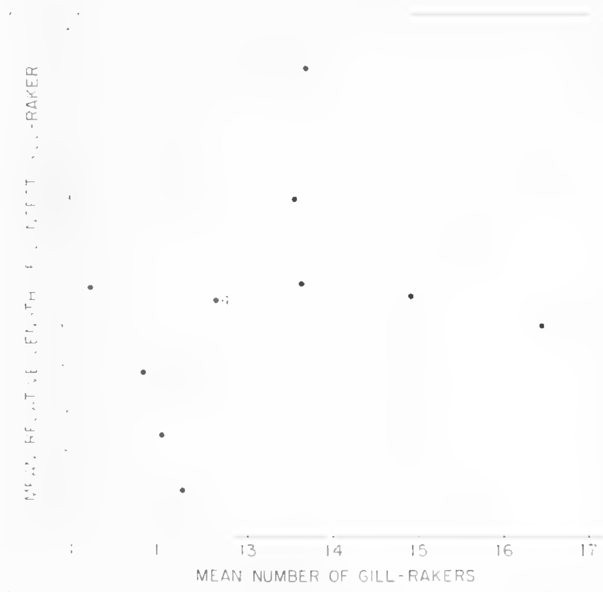


FIGURE 29. Correlation between mean number of gill-rakers (from table 22) and mean relative length of longest raker (from table 25), in various populations of *Gila bicolor* in Nevada. The numerals on the graph represent the Locations, G1 to G11 (listed on table 22).

but are definitely longer than in typical '*obesa*,' moderately so at Birch Ranch (G5) and strikingly so (fig. 28B) at Sulphur Spring (G6). With some variation, both lengths and numbers are low in the subspecies *G. b. newarkensis* (G7, 8; fig. 28C) and *G. b. euchila* (G10) of the basin of Lake Newark. Median length and the lowest mean number characterize *G. b. isolata* (G11) of Independence Valley.

The form and texture of the rakers are also subject to marked differences, as is indicated especially in the descriptions of *G. b. newarkensis* (p. 168) and the Sulphur Spring race of *G. b. obesa* (p. 156).

PHARYNGEAL TEETH. In the vast area comprising the many basins that were demonstrably or putatively part of the watershed of Lake Lahontan at the height of the late pluvial period, or are thought somehow otherwise to have derived their *Gila bicolor* stock from the Lahontan drainage basin, the number of these teeth (table 23) looms in importance. One reason is that the two main Lahontan forms, *G. b. obesa* and *G. b. pectinifer*,

TABLE 23. *Number of pharyngeal teeth in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality	No. on left side					No. on right side					No. on either side					
	4[1]	5	6[2]	No.	Mean	3[3]	4	5[4]	No.	Mean	3	4	5	6	No.	Mean
Gila bicolor obesa																
Lake Lahontan																
Carson River[5]	2	35	2	39	5.00	—	25	6[5]	31	4.19	—	27	33	2[2]	62	4.58
Humboldt River																
Near Lovelock	2	40	—	42	4.95	—	38	4	42	4.10	—	40	44	—	84	4.52
Near Carlin	3	12	—	15	4.80	—	14	1	15	4.07	—	17	13	—	30	4.43
Bishop Creek	1	14	—	15	4.93	1	14	—	15	3.93	1[3]	15	14	—	30	4.43
Lake Diamond																
Birch Ranch	1	14	—	15	4.93	—	15	—	15	4.00	—	16	14	—	30	4.47
Sulphur Spring	—	15	—	15	5.00	—	15	—	15	4.00	—	15	15	—	30	4.50
Gila bicolor newarkensis																
Lake Newark																
Near Diamond Peak	2	13	—	15	4.87	—	14	1	15	4.07	—	16	14	—	30	4.47
Moores Ranch	3	12	—	15	4.80	—	13	2	15	4.13	—	16	14	—	30	4.47
Warm Springs	—	4	—	4	5.00	—	4	—	4	4.00	—	4	4	—	8	4.50
Gila bicolor euchila																
Lake Newark																
Fish Creek Springs	—	15	—	15	5.00	—	15	—	15	4.00	—	15	15	—	30	4.50
Gila bicolor isolata																
Lake Clover																
Independence Valley	2	13	—	15	4.87	—	15	—	15	4.00	—	17	13	—	30	4.43
Totals	16	187	2	205	4.93	1	182	14	197	4.07	1	198	193	2	394	4.50

differ in this respect (as well as in the numbers of gill-rakers and pelvic rays, and in various features of form).

Gila bicolor obesa (pp. 153, 156), the more widespread type, typically inhabiting streams and springs, normally has 5—4 teeth (that is, 5 on the left arch and 4 on the right), and this is true also of the modified derivatives of *G. b. obesa* in the enclosed basins just south of the Humboldt River system (table 1). Rarely the numbers are reversed, 4—5, or the same number occurs on both sides. When symmetrical in number, the teeth are more often 4—4 than 5—5, except where, as in the samples from Carson River near Fallon and from Humboldt River near Lovelock, introgression from '*pectinifer*' has apparently increased the proportion with 5—5 teeth. In the sample from Bishop Creek we have found a variant with 4—3 teeth. Reduction to 3 teeth, in this case on the left arch (formula 3—4) was found (along with one of 4—4) among 10 counts for the introduced stock of *Gila bicolor obesa* in Little Soda Lake, Nevada.

In contrast, the teeth normally number 5—5 in the lacustrine form, which Snyder (1917, pp. 64–67, figs. 5, 6) regarded as generically as well as specifically distinct, under the name *Leucidius pectinifer*, but which, by reason of evidence of extensive introgression and intergradation (pp. 143–149), we separate only subspecifically, as *Gila bicolor pectinifer*. Snyder stated that the teeth in this form are invariably 5—5, but we find some with 5—4.

Precautions in the counting of the pharyngeal teeth when some have been lost are mentioned on page 93).

SUBSPECIES STATUS OF ISOLATED FORMS. We combine within one species, *Gila bicolor*, not only the ecologically segregated forms discussed above as *G. b. obesa* and *G. b. pectinifer*, but also all of the hitherto described, isolated local forms, including those of the Death Valley system (Miller, 1973), that have been referred to *Siphateles* (and may be retained in a subgenus of that name). We have proposed three additional subspecies.

All of these forms, plus a considerable number that remain to be named, have many features in common, though they differ greatly in the number

TABLE 23. CONTINUED.

Subspecies Pluvial lake system Locality	Total number of teeth						Tooth formulas[6]						Asymmetry[7]	
	7[3]	8	9	10	No.	Mean	4–3[3]	4–4	4[1]–5[4]	5–4	5–5[4]	6[2]–4	100(L+R) No.	100R L+R
Gila bicolor obesa														
Lake Lahontan														
Carson River[5]	—	—	25	6[5]	31	9.19	—	—	2	23	4[5]	2	87	7
Humboldt River														
Near Lovelock	—	2	36	4	42	9.05	—	2	—	36	4	—	90	0
Near Carlin	—	3	11	1	15	8.87	—	3	—	11	1	—	73	0
Bishop Creek	1	—	14	—	15	8.87	1[3]	—	—	14	—	—	100	0
Lake Diamond														
Birch Ranch	—	1	14	—	15	8.93	—	1	—	14	—	—	93	0
Sulphur Spring	—	—	15	—	15	9.00	—	—	—	15	—	—	100	0
Gila bicolor newarkensis														
Lake Newark														
Near Diamond Peak	—	2	12	1	15	8.93	—	2	—	12	1	—	80	0
Moores Ranch	—	2	12	1	15	8.93	—	2	1	11	1	—	80	0
Warm Springs	—	—	4	—	4	9.00	—	—	—	4	—	—	100	0
Gila bicolor euchila														
Lake Newark														
Fish Creek Springs	—	—	15	—	15	9.00	—	—	—	15	—	—	100	0
Gila bicolor isolata														
Lake Clover														
Independence Valley	—	2	13	—	15	8.87	—	2	—	13	—	—	80	0
Totals	1	12	171	13	197	8.99	1	12	3	168	11	2	88	2

[1] When the number of teeth is reduced to 4 on the left side, tooth no. 1 (uppermost) is usually more or less disproportionately massive.
[2] In the two specimens with 6 teeth in the major row on the left arch the seriation of the teeth is slightly irregular, as is indicated in the text.
[3] In the specimen with 4—3 teeth there is evidence (see text) that there was not quite enough room for the uppermost tooth to fit.
[4] When 5 instead of 4 teeth develop on the right side, and sometimes when 5 form on the left arch, the uppermost tooth is more or less reduced and displaced outward, more or less against the side of the second tooth.
[5] The population from the Carson River near Fallon represents *G. b. obesa* modified by introgression from *G. b. pectinifer*. This is reflected by the increased number of fish with 5 teeth on each side (a characteristic of *G. b. pectinifer*, but otherwise essentially like the other specimens in the series.
[6] In the tooth formula the left side is represented first.
[7] The indices, as proposed by Hubbs and Hubbs (1945, pp. 231–233), specify (1) the degree of asymmetry in the count and (2) among asymmetrical counts, the percentage of extrality (normally the count on the left side is one higher than on the right side).

of gill-rakers. No specimen in the entire complex has ever been found to have teeth in other than the main row. In all, the better developed scales have a distinctive form: shield-shaped, with focus far basad, typically with apical radii only, circuli well spaced in the apical field, moderately crowded laterally, and densely crowded basally; with strong anterolateral angles, and with the anterior margin and anterior circuli arched inward toward each anterolateral angle (as illustrated on fig. 46A and by Kimsey, 1954, fig. 4); some scales, however, are more nearly vertically oval, without sharp angulation. As a rule, the various local forms are moderately large and have relatively uniform contours, proportions, and colors (figs. 30, 31, 35A,B). The range of the species, though in arid areas rather scattered, is relatively compact.

When considered alone, some of the localized forms seem sufficiently distinctive to lead one to question whether full specific separation would not be proper, but when the whole array of forms is kept in mind, subspecies status seems preferable. No two forms of the complex, other than '*obesa*' and '*pectinifer*,' are anywhere sympatric.

LOCAL POPULATIONS OF *GILA BICOLOR* EXAMINED

The populations of *Gila bicolor* treated in detail in the present study, all in Nevada, are referred to four subspecies (listed also, briefly, in table 21):

TABLE 24. *Correlation of gill-raker number with the tooth patterns characteristic of* Gila bicolor obesa *(5–4) and of* G. b. pectinifer *(5–5) for two Locations in the Lahontan system.*

Location G1, Carson River near Fallon (UMMZ 124859)

Tooth formula	Gill-raker number (both sides counted)												
	12	13	14	15	16	17	18	19	20	21	22	23	No.	Ave.
5—4 (rarely 4—5)	1	5	5	10	10	4	2	4	4	1	3	1	50	16.72
5—5	—	—	—	—	1	3	2	1	1	—	—	—	8	17.75

Location G2, Humboldt River near Lovelock (UMMZ 124873, 124874)

Tooth formula	Gill-raker number (both sides counted)								
	12–16	17	18	19	20	21	22	No.	Ave.[1]
5—4	64	3	—	1	2	1	1	72	15.46
5—5	2	—	4	—	—	1	1	8	18.13

[1] Average computed on assumption that the raker number for the entire 12–16 mm. grouping was the modal number, 15 (table 22).

(A) *G. b. obesa* (Girard), represented by samples from the following Locations:
- G1: Carson River near Fallon, near central part of Lake Lahontan drainage basin.
- G2: Humboldt River near Lovelock, on the bed of Lake Lahontan.
- G3: Humboldt River near Carlin, above the bed of Lake Lahontan.
- G4: Bishop Creek, a headwater of Humboldt River, near Wells.

(A′) *G. b. obesa*, aberrant races:
- G5: Birch Ranch, on east side of Diamond Valley.
- G6: Sulphur Spring, on west side of Diamond Valley.

(B) *G. b. newarkensis* Hubbs and Miller, represented by samples from three Locations on the bed of pluvial Lake Newark:
- G7: Spring near Diamond Peak, on west side of Newark Valley.
- G8: Spring-fed pool at Moores Ranch, on west side of Newark Valley.
- G9: Warm Springs, near north end of Newark Valley.

(C) *G. b. euchila* Hubbs and Miller, from a single Location, also in the basin of Lake Newark:
- G10 and 10A: Fish Creek Springs, in Fish Creek Valley.

(D) *G. b. isolata* Hubbs and Miller, represented from a single Location in the basin of pluvial Lake Clover:
- G11: Warm Springs, Independence Valley.

On the several maps (figs. 3, 8, 12) involved, the Locations (the extralimital G1 and G2 excepted) are marked, in the sequence of the preceding enumeration, by the designations G3 to G11.

The seemingly remote possibility that some form of *Gila bicolor* (it would most plausibly have been *G. b. obesa*) occurred until recently in Ruby Lake of the Lake Franklin basin is suggested by local testimony (p. 209).

LAHONTAN CREEK TUI CHUB

Gila bicolor obesa (Girard).

(Figure 30.)

As mentioned in the preceding account of the species, we treat the trophically differentiated stream and lake forms of the subgenus *Siphateles* in the Lahontan system and related drainage basins, namely '*obesa*' and '*pectinifer*,' as subspecifically rather than as specifically distinct (or as taxonomically inseparable). Our study of the entire complex has further suggested that the stream form of the Lahontan system is subspecifically separable from *Gila bicolor bicolor* of Klamath Lake, Oregon.

Because the populations of *Gila bicolor* that occur in isolated waters within the area of Nevada included in this report all give evidence of having been derived from stocks of *G. b. obesa* (or an immediate ancestor) of the Humboldt River system, we have included in our analysis, as we did

for *Rhinichthys osculus*, samples from that system taken to represent the form ancestral to the now isolated stocks. Location G2 is from near Lovelock, close to the lower end of the river, on the bed of Lake Lahontan, probably from near where the types were collected. Location G3 is from midcourse of the Humboldt River, near Carlin. Location G4 is from a headwater tributary, Bishop Creek. We have incorporated also data for a collection (G1) from the Carson River near Fallon, also on the bed of Lake Lahontan, to represent a stock of *G. b. obesa* that appears to have been modified by introgression from the lacustrine form, *G. b. pectinifer*.

Populations of Carson River and Humboldt River Systems.

Location G1.—**Carson River**, in T. 19 N., R. 28 E.; Churchill County, 2 miles west of Fallon, Nevada, on the bed of Lake Lahontan (west of the limits of fig. 1). Rather muddy water (bottom visibility about 0.3 m.); mud and gravel bottom; pools and riffles; scanty growth of *Myriophyllum* and *Potamogeton*; 20° C. (air 31°). Stream here 7–20 m. wide and to 0.6 m. deep. Hubbs family and Miller, July 30, 1938 (M38-77); UMMZ 124859 and 133244 (35, 28–136 mm.); 25-foot seine with ¼-inch square mesh in bag. Associated species were four other natives (*Catostomus tahoensis, C. platyrhynchus, Rhinichthys osculus robustus, Richardsonius egregius*) and four exotics (*Ictalurus m. melas, Perca flavescens, Micropterus salmoides*, and *Archoplites interruptus*).

Location G2.—**Humboldt River near Lovelock**, at Irish American Dam, in T. 27 N., near boundary of R. 31–32 E.; Pershing County, Nevada, about 3 miles northeast of Lovelock, on the bed of Lake Lahontan (west of fig. 1). Water olive-yellow and muddy (bottom visibility ca. 15 cm.); mostly firm to soft clay, with fine gravel in riffles; pool-and-riffle; scanty growth of *Potamogeton*, cf. *P. pectinatus*; 23° C. (air 32°). Stream here 5–20 m. wide and to ca. 1 m. deep. Hubbs family and Miller, July 31, 1938 (M38-79); UMMZ 124873–74 (111, 20–115 mm.); 25-foot seine with ¼-inch square mesh in bag. Some of the young and half-grown from the backwater had mud on gills. Four other native fishes, *Catostomus tahoensis, C. platyrhynchus* (as well as hybrids between the two suckers), *Rhinichthys osculus robustus*, and *Richardsonius egregius*, and three exotic species (*Cyprinus carpio, Ictalurus n. nebulosus*, and *I. m. melas*) were collected.

Location G3.—**Humboldt River near Carlin**, just above hot springs along and in river bed, in T. 33 N., R. 52 E.; Elko County, Nevada, ca. 1.0 mile southwest of Carlin (figs. 1, 8). Rather murky (clay limiting bottom underwater visibility to ca. 0.5 m.); clay, sand, and mud, with gravel on riffle; pool, riffle, and backwater slough; no vegetation; 23° C. (air 33°). Hubbs family and Miller, August 11, 1938 (M38-119); UMMZ 124915 (40, 27–107 mm.); 25-foot seine with ¼-inch square mesh in bag. Associated species were four other natives (*Catostomus tahoensis, C. platyrhynchus, Rhinichthys osculus robustus, Richardsonius egregius*) and three exotics (*Cyprinus carpio, Ictalurus n. nebulosus, I. m. melas*).

Location G4.—**Bishop Creek**: described (p. 107) under Location R2 (fig. 12); UMMZ 141523 (254, 17–137 mm.). Young to adult abounded. The young swarmed along margins of pond. Some of the females, taken off a large gravel riffle, were running-ripe. Three other native fishes were obtained (*Catostomus tahoensis, Rhinichthys osculus robustus, Richardsonius egregius*).

The Lahontan populations sampled, one from Carson River and three from the Humboldt River system, are by no means uniform in systematic characters. In most respects the characters form a downstream–upstream cline. In some respects, notably gill-raker number, the cline in the downstream direction verges toward *Gila bicolor pectinifer*. The cline in the upstream direction approaches the forms that inhabit the endorheic basins just south of the Humboldt River.

In the following analyses the variation, whether or not clinal, is treated in the upstream direction, taking the Carson River sample first (G1 → G2 → G3 → G4).

Size. The maximum standard lengths in this series are 136 → 115 → 107 → 137 mm. Rather contrary to expectation, no significant trend is indicated.

Coloration. The coloration is essentially plain and, as the species name implies, bicolored: pigmented on the back and midsides and silvery below (figs. 30A–C). The bicolored condition and the general light tone is more conspicuous in the downstream Locations (G1 and G2); in the two upstream Locations (G3 and G4) the fish are duskier and the puncticulate area extends farther

down, leaving little but the transverse ventral region silvery. In the series as outlined, there is a gradation in the pigmentation along the middle of the trunk, from a pattern essentially margining the silvery centered, vertically diamond-shaped scale pockets to one more evenly darkened. There in a striking upstream gradient in the shape and intensity of the basicaudal spot, which is higher than long, pointed forward, and truncate behind: it is strong in the Carson River sample, somewhat weaker and more diffuse in the collection from near Lovelock, weak to diffuse or small in the Carlin lot, and barely evident in the Bishop Creek collection.

In all series, the head is dark on top, on the snout, around the lower border of the eye, and on the upper part of the opercular region; large melanophores are conspicuous on the cheek, the opercular region, and the lower sides. In all series, the dorsal and caudal fins are dusky and in nearly all specimens there is some puncticulation on all lower fins.

As in all forms of *Gila bicolor* here treated, a rather diffuse underlying midlateral dark streak is developed in young fish, but tends to become obscure or obsolete in adults; the young also show scattered large melanophores on the lower sides—a distinctive feature of the whole species.

Life colors. The field notes indicate that at least one of the specimens taken near Carlin had the center of the lower fins rusty orange, and that the males collected at Bishop had some gilt on the sides and the lower fins brownish tan inside light margins.

Form. The general form (figs. 30A–C) grades in the stated series from one that downstream is rather strongly compressed and sharp-snouted, to one upstream that is more chubby and turgid, with a somewhat rounder snout in both side and top view. The fins grade, in the same direction, from slightly falcate to moderately rounded.

Lateral-line system. Ordinarily, the lateral line on the body is complete in *G. b. obesa*.

The supratemporal canal (table 26) is more often incomplete than complete in these four collections, but only slightly so at Location G2 near Lovelock.

Morphometry. For all three Locations in the Humboldt River system, the morphometric data (table 27) were compared between smaller and larger specimens of each sex, within standard-length groupings, of 45–98 and 100–137 mm. for females and of 48–73 and 74–107 mm. for males (one 76-mm. male from Bishop Creek was included in the smaller category, because no others in the large category are available). Within the downstream-to-upstream series the proportional measurements show for each sex an increase in the predorsal length, in line with a trend toward a posterior position of the dorsal fin in isolated waters, a slight increase in head size, and, in line with expectation, a definite decrease in average size of fins.

The mean values for proportional predorsal length (fig. 36) for the Humboldt River samples are relatively lower than in the isolated subspecies, and the mandible (figs. 34, 37) averages shorter than in *G. b. euchila* and *G. b. isolata*.

Sexual dimorphism and nuptial characters. In the three series from the Humboldt River system the sexual dimorphism is rather limited, though in the usual direction (table 28). The dorsal fin usually averages less posterior in males, but the difference is small except for the larger fish from near Lovelock. The enlargement of the paired fins in the males is about average: the excess of the means in the males, in terms of percentage of the standard length, is 0.1–1.6 for the dorsal, 0.4–0.8 with one obviously unrepresentative figure of 4.4 for the caudal, 2.2–3.4 for the pectoral, and 0.8–1.6 for the pelvic. The moderate size of the pectoral fin in the males of *G. b. obesa* is emphasized by comparing the values for this subspecies with those of *G. b. newarkensis* (fig. 32).

A 76-mm. nuptial male from Bishop Creek displays nuptial tubercles similar to those described for *G. b. isolata* (p. 179).

Fin rays. Rays were counted (tables 29, 30) on all four series from the present Lahontan drain-

age system. In the entire lot, the dorsal-ray counts seldom vary from 8. The number of anal rays decreases slightly on the average upstream to Carlin, in slight approach toward the number, modally 7, in the subspecies confined to isolated springs, but seems to revert to a slightly higher average in Bishop Creek. The caudal rays vary from 17 to 20, with few variants from 19. The pectoral-ray mean decreases slightly in the upstream gradient within the Humboldt River system, but is about average in Carson River. The pelvic-ray mean fluctuates slightly: 9.49 near Lovelock, 9.29 near Carlin and in Bishop Creek, and only 9.21 in Carson River (which is surprising, because this series showed signs of introgression from *G. b. pectinifer*, which usually has 10 pelvic rays).

VERTEBRAE. The vertebral counts (table 31) fluctuate slightly and irregularly.

SCALE ROWS. The average for the 11 scale counts (table 32) is uniformly highest in Carson River, which may reflect the higher number in *G. b. pectinifer*. The sequence in the downstream-upstream series (G1 to G4) was either $2 \rightarrow 4 \rightarrow 3 \rightarrow 1$ or $4 \rightarrow 2 \rightarrow 3 \rightarrow 1$.

GILL-RAKERS. The raker counts (table 22) exhibit a very sharp upstream decrease, in a regular cline, with means of $16.43 > 14.90 > 13.62 > 12.61$. As noted above, we attribute the higher number downstream to past hybridization with *G. b. pectinifer*, which has 29 to 40 rakers, and subsequent backcrossing with *G. b. obesa*. The strong positive skewness of the counts for Carson River and for Humboldt River at Lovelock, with a long gradual tail in the distribution, is a major consideration in our interpretation. Especially notable is the lack of positive skewness for the two upstream collections, far removed from contamination with *G. b. pectinifer*. The finding of intergrades between *G. b. obesa* and *G. b. pectinifer* in ancient fish caches of Indians in the Lovelock region, as we have pointed out (Hubbs and Miller, 1948b, p. 41), demonstrates past intermixing near the lower end of Humboldt River. The collections from Carson River near Fallon and from Humboldt River near Lovelock appear to represent largely reintegrated populations, rather than a mixture of *G. b. obesa* with F_1 hybrids between *G. b. obesa* and *G. b. pectinifer*. The extreme upper end of the counts in the two series is about midway between the mean for *G. b. obesa* and the midpoint between the means for the two forms, and the close similarity to *G. b. obesa* of the individuals with high raker counts suggests to us past backcrossing with *G. b. obesa*, the locally dominant form.

The gill-rakers in the Humboldt River system are of moderate length, shorter than in the Diamond Valley populations of *G. b. obesa* and longer than in *G. b. newarkensis* and *G. b. euchila* (table 25; fig. 28).

PHARYNGEAL TEETH. Influence of *G. b. pectinifer* in the collections from Carson River near Fallon and from Humboldt River near Lovelock seems to be indicated also by the somewhat higher than usual proportion of pharyngeal arches with the 5—5 tooth formula of the lake form—more frequently 5—5 in these collections than in any other populations here treated (table 23). That the specimens with 5—5 teeth have almost the same raker number as those with 5—4 teeth in the Carson River sample and a not much higher raker number in the sample from near Lovelock, however, is shown by correlating the tooth and raker counts (table 24). The dental formula in these samples, especially the one from Carson River, is also more variable than in other samples, which in this regard are essentially uniform.

ABERRANT POPULATIONS, OF THE PLUVIAL LAKE DIAMOND BASIN, REFERRED TO *Gila bicolor obesa*.

The two populations in this category occur within the sump of the extensive drainage basin of pluvial Lake Diamond, close to the margin on the ancient lake, one on the west side and one on the east side. Field reconnaissance, with frequent interviews, yielded no seemingly reliable indication that tui chubs (*Gila bicolor*) occur in the

TABLE 25. *Length of longest gill-raker in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality[2]	Length of rakers[1] in permillage of standard length[3]							
	7.5–11.5	11.5–15.5	15.5–19.5	19.5–23.5	23.5–27.5	27.5–31.5	N	M[4]
Gila bicolor obesa								
Lake Lahontan								
Carson River (1)	1	14	16	3	—	—	34	15.8
Humboldt River								
Near Lovelock (2)	—	10	41	3	—	—	54	16.7
Near Carlin (3)	—	8	35	3	—	—	46	17.0
Bishop Creek (4)	—	11	24	3	—	—	38	16.6
Lake Diamond								
Birch Ranch (5)	—	4	11	10	1	—	26	19.0
Sulphur Spring (6)	—	2	9	25	18	3	57	22.1
Gila bicolor newarkensis								
Lake Newark								
Near Diamond Peak (7)	9	37	8	—	—	—	54	13.4
Moores Ranch (8)	16	23	—	—	—	—	39	12.1
Gila bicolor euchila								
Lake Newark								
Fish Creek Springs (10)	3	30	25	—	—	—	58	14.9
Gila bicolor isolata								
Lake Clover								
Independence Valley (11)	1	10	40	5	—	—	56	16.9

[1] Measured on one side from hard base to tip.
[2] Expressed as numbered Locations in the G series.
[3] Values grouped in classes of four units; mean values of units are listed.
[4] Means determined from ungrouped data.

tributary basins to the west and southwest, where two populations of *Rhinichthys osculus* were discovered. Our field work convinced us that on the east side of Diamond Valley chubs occurred only at Birch Ranch (Location G5), along with *Rhinichthys osculus* (p. 115). On the west side we found them only in Sulphur Spring (G6, where it alone occurred), and determined it to be lacking in Big Shipley Spring, which harbored *Rhinichthys* (Location R8). No definite indication was obtained, by local inquiry or examination, of the occurrence of *Gila bicolor* elsewhere on the west side of Diamond Valley, but the possibility remains that some may have held out in some of the springs we did not examine (pp. 18–19). We did hear one vague report of fish called "chubs" in a spring hole in the yard of Bailey Ranch 3.2 km. south of Big Shipley Spring. We think it probable that only the two populations, or at least types, of *Gila bicolor* persist (or occurred in 1938) anywhere in the wide arid expanse of the ancient Lake Diamond drainage basin of Nevada.

Location G5.—Springs on **Birch Ranch**: described (p. 115) under Location R7 (figs. 3, 8). UMMZ 124934 (113, 15–81 mm.). The presumably indigenous occurrence of this chub here, and its close association with *Rhinichthys osculus*, are discussed on the same page.

Location G6.—**Sulphur Spring**, on the west side of the extensive flat of Diamond Valley, just below the foot of the Sulphur Spring Range, shown on the Garden Valley 15-minute Quadrangle as near the western edge, submedially, of Sec. 36, T. 23 N., R. 52 E.; eastern Eureka County, Nevada, 8.7 miles by road south of Sadler Ranch (figs. 3, 8). Somewhat sulphurous, and clear but easily roiled; very soft pulpy peat; no current; much algae, rushes, etc.; 22° C. (air 28°). Hubbs family and Miller, August 12, 1938 (M38-122); UMMZ 124927–28 (71, 21–86 mm.); 6-foot woven-mesh seine and 15-foot seine with 1/4-inch square mesh.

The Sulphur Spring population seems to be rigidly confined to the somewhat dammed spring pool which was about 10 m. in diameter and about 0.3 m. deep to an ill-defined bottom. No fish were in the irrigation ditch leading out from the pool. Algae were observed in the feces of the fish.

In consonance with the evidence of a rather late-pluvial outlet of Lake Diamond (pp. 16–17), the two populations of Diamond Valley are referred to the Lahontan creek tui chub, *Gila bicolor obesa*. However, the Sulphur Spring population (G6) would have been separated subspecifically, chiefly on the basis of its unusually long gill-rakers (table 25; fig. 28B), had we not found that the Birch Ranch series (G5) bridges the gap. Differences between the two isolated spring populations of Diamond Valley, as specified below, indicate considerable modification of the Diamond Valley stock since Lake Diamond ceased discharging in presumably rather late pluvial time, and also suggest some differentiation since Lake Diamond desiccated beyond conditions viable for fish, probably only a few thousand years ago.

SIZE. Consistent with the highly restricted habitat, the two populations are rather dwarfed. The largest specimens, as now preserved, are 81 and 86 mm. in standard length, respectively, as compared with 107–137 mm. for the samples from Carson and Humboldt rivers.

COLORATION. The general coloration (fig. 30D) in both lots is essentially the same as in the upstream samples of the Humboldt River system. The basicaudal spot varies from moderately strong to minute and/or diffuse, or even lacking. It is apparently never vertically elongate, with a definite anterior angle and a sharply truncate posterior edge, as it is in the two downstream population discussed above.

LIFE COLORS. The colors of the Sulphur Spring fish were described as follows in the field, and it was noted that those from Birch Ranch were similar: rather bright olive on back, passing through more or less definite gilt reflections on midsides to bluish white on lower parts. Dorsal and caudal fins olive. Lower fins olive, grading toward yellowish, with only a trace of a bluish border on pelvic and anal. Axil of pectoral fin and exposed part of shoulder girdle more or less golden, with a pinkish tinge in some. Iris bright gold around pupil. These colors seem to have been somewhat modified from those displayed by the tui chubs in the Humboldt River and its tributaries.

FORM. The Birch Ranch specimens are shaped much like those from Bishop Creek, with moderately turgid body contours. The Sulphur Spring fish (fig. 30D) tend to be rather more compressed, to have the dorsal contour more elevated, the muzzle more pointed, and the mouth more oblique and straighter (which may be correlated with the extreme development of the gill-rakers). The fins are about as rounded as in the upstream end of the cline in the Humboldt River system.

LATERAL-LINE SYSTEM. Ordinarily, the lateral line on the body is complete in each population in Diamond Valley.

The supratemporal canal (table 26) seems to be uniformly incomplete in both collections from Diamond Valley, as in no other area treated in this study. This circumstance lends support to the view that the two populations have had a common origin. In many of the specimens, the canal has

TABLE 26. *Condition of supratemporal canal (complete or incomplete) in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies Pluvial lake system Locality	Supratemporal canal Complete	 Incomplete
Gila bicolor obesa		
Lake Lahontan		
Carson River	6	24[1]
Humboldt River		
Near Lovelock	20	28
Near Carlin	6	24[2]
Bishop Creek	12	26
Lake Diamond		
Birch Ranch	—	29[3]
Sulphur Spring	—	35[3]
Gila bicolor newarkensis		
Lake Newark		
Near Diamond Peak	24	6
Moores Ranch	21	9
Gila bicolor euchila		
Lake Newark		
Fish Creek Springs	17	6
Gila bicolor isolata		
Lake Clover		
Independence Valley	27	—

[1] One break in 14, 2 breaks in 6, and 3 breaks in 4.
[2] One break in 12, 2 breaks in 5, and 3 breaks in 7.
[3] In many specimens the canal has 3 breaks, one at midline and one on each side.

three breaks, one at the midline and one on each side.

MORPHOMETRY. Distinctive features in body, head, or fin proportions (table 27) are few. The body seems to average deeper in the Diamond Valley series than in those from Humboldt River. The head in the Sulphur Spring specimens, but not in those from Birch Ranch, averages longer than in the Carson-Humboldt samples. The fins in the Sulphur Spring fish average somewhat larger than in those from Birch Ranch and definitely larger than in the more upstream Carson-Humboldt samples.

SEXUAL DIMORPHISM. Almost no sexual dimorphism is indicated for the body, head, and vertical-fin measurements (table 28). For pectoral-fin length the excess values for the males, expressed as percentage of the standard length, are 2.6 and 1.8 for the pectoral fin for the Birch Ranch and Sulphur Spring collections, respectively. Corresponding values for the pelvics are 1.4 and 0.9. These values compare closely with those for the present Lahontan drainage. The enlargement of the fins in the male in these series is indicated by the measurements to be small for the dorsal fin, dubious for the caudal, and about average for the paired fins.

FIN RAYS. The ray counts for the vertical fins (table 29) are not distinctive. The counts of pectoral rays (table 30) average very slightly lower in the Sulphur Spring than in the Birch Ranch sample, but fit within the variation for the Humboldt samples. The average for the pelvic-ray counts is very slightly reduced in the Sulphur Spring fish, as contrasted with the other samples referred to *G. b. obesa.*

VERTEBRAE. Not distinctive (table 31).

SCALE ROWS. The scale-count averages (table 32) for all 11 sets are virtually identical for the two Diamond Valley samples, and generally fit within the variation for the samples more typical of *G. b. obesa.* The counts of predorsal scales and of scales around body average slightly lower than for the Humboldt River Locations.

GILL-RAKERS. The raker counts (table 22) are very slightly higher on the average in the Sulphur Spring than in the Birch Ranch sample, and correspond closely with the mean for the Carlin sample, in the sharp cline of the Carson-Humboldt series. The averages are definitely lower than in the Lovelock downstream sample and are distinctly higher than in the Bishop Creek headwater sample.

As already mentioned, the rakers in the Sulphur Spring sample are so outstandingly long (table 25; fig. 28B) that a subspecies would have been erected for it, had not the Birch Ranch fish been so definitely intermediate in this respect between the Sulphur Spring sample and all others referred to *Gila bicolor obesa*: 81 percent of the raker measurements for the Sulphur Spring sample, expressed as permillage of the standard length of the fish, are barely overlapped by less than 10 percent of the values for any of the four samples from the Carson and Humboldt localities, but in this respect the Birch Ranch fish are just intermediate.

The gill-rakers of the Sulphur Spring tui chubs also differ in form and structure (fig. 28B) from those of approximately topotypic *G. b. obesa*, as represented by the Lovelock series. They remain bony and slender to their well separated bases, and there are usually some crenulations along the inner edge. In typical *G. b. obesa* the rakers (fig. 28A), especially in small specimens, grade in appearance from those of *G. b. newarkensis* (p. 168; fig. 28C) to those of the Sulphur Spring sample (fig. 28B).

PHARYNGEAL TEETH. The dentition of the Diamond Valley populations is essentially like that of *G. b. obesa.* Among 15 specimens examined for each population the only variant from 5—4 is one from Birch Ranch with 4—4.

NEWARK VALLEY TUI CHUB

Gila bicolor newarkensis Hubbs and Miller.
(Figure 31A,B.)

Gila bicolor newarkensis HUBBS and MILLER, 1972, p. 102 (diagnosis).

All indications point to the conclusion that this subspecies is confined to the main depression,

Newark Valley proper, in the drainage basin of pluvial Lake Newark (pp. 22–26; figs. 3, 8), in the western part of White Pine County, Nevada, and that it is the only native fish in the main depression. The form occurring in Fish Creek Springs, in Fish Creek (Little Smoky) Valley, the southwestern arm of the same drainage basin, is regarded as constituting a differentiated subspecies, *Gila bicolor euchila* (pp. 168–174). Populations of *G. b. newarkensis* have been taken in only three springs, with data as follows:

Location G7.—Spring in Newark Valley on west side, **near Diamond Peak** (called "South Peak" locally in 1934), on alluvial slope about opposite south end of Newark Dry Lake, now thought to be at or near Circle Ranch as shown on the Eureka 15-minute Quadrangle and as Labarry Ranch on a county map of 1959, or at one of the springs mapped for about 2 km. south and southwest of that ranch, near middle of T. 20 N., R. 55 E.; in northwestern White Pine County, Nevada (figs. 3, 8). Clear water; soft bottom (person sank about 15 cm.); seepage overflow; *Chara* forming a thick mat on bottom, algae and some *Nasturtium* blanketing surface; water cool; pool ca. 7 × 12 m. and ca. 0.6 m. deep. Hubbs family, September 11, 1934 (M34-206); UMMZ 132185 and 188893 (227, 25–97 mm.); 15-foot seine with ¼-inch square mesh. Some extremely young fish seen here (and at G8) indicated late spawning in the cold water.

Location G8.—Spring-fed pool on west side of Newark Valley, on **Moores Ranch**, apparently the one named Goecoechia Ranch on the Diamond Springs 15-minute Quadrangle, and probably one of the pools shown between the 5,860-foot and 5,880-foot contours in SW ¼ Sec. 11 and NW ¼ Sec. 14, T. 22 N., R. 55 E., in northwestern White Pine County, Nevada, by road 6 miles north of Strawberry (Strawberry Ranch) and 5 miles south of Simonsen, also known as Simonsen Ranch or Cold Creek Ranch (figs. 3, 8). Clear water; soft mud; virtually no current; only a few open spots in dense *Nasturtium*, with *Chara* thick below; water cold. Hubbs family, September 11, 1934 (M34-207); UMMZ 132186 (113, 20–67 mm.); 15-foot seine with ¼-inch square mesh.

Location G9.—Ditch fed by **Warm Springs**, on what was known as "Billy Moore's Ranch," on the very gentle alluvial slope in the eastern lobe at the north end of Newark Valley, apparently between the 5,880-foot and 5,920-foot contours shown on the Cold Creek 15-minute Quadrangle in the SE ¼ Sec. 36, T. 23 N., R. 56 E.; in northwestern White Pine County, Nevada (figs. 3, 8). Clear water; soil bottom; moderate current; little vegetation; "not quite lukewarm." Hubbs family, September 11, 1934 (M34-208); UMMZ 132187 (10, 19–31 mm.); 6-foot woven-mesh seine.

The sample of young fish at Location G9 was quickly taken, with the idea of merely ascertaining whether the fish here are the same as those in the colder springs on the west side of the valley (Locations G7 and G8), which were assumed to represent an undescribed form. The fish were caught in a sheet-piled ditch about 0.6 m. wide. The rancher, Billy Moore, as was widely known, kept goldfish (*Carassius auratus*) of varied hues, carp (*Cyprinus carpio*), and catfish (*Ictalurus* sp.). From afar it had been recommended that we examine the spring-fed waters of this ranch.

We think that we may have sampled the only then extant stocks of native fish on the east side of the valley and the two populations, perhaps all that existed, in the northern part of the west side (the southern part apparently has no waters capable of having retained fish life). The two western Locations, G7 and G8, probably lie at or near the southern and northern limits of the fish-inhabited springs. Roughly midway between, at Strawberry Ranch (in SW ¼ Sec. 10, T. 21 N., R. 55 E.), we were informed on September 11, 1934, by the lady rancher, that her springs, then about dry in the extreme drought of that year, had contained minnows, but that they had been destroyed by freezing a few years previously, dying in such numbers that they emitted a terrible stench when the ice thawed. Thereafter, she said, no minnows were observed. Numerous springs between Strawberry Ranch and the spring that yielded sample G7 are shown on the Eureka 15-minute Quadrangle, and we suspect that they may prove to contain minnows, probably much like those taken at Location G7.

A streamlet about 1.5 m. wide, with *Nasturtium*, named Cold Creek on Cold Creek Ranch 15-minute Quadrangle, was found to be fishless where examined near Simonsen (now Cold Creek) Ranch on September 11, 1934. This stream is shown on the Diamond Springs 15-minute Quadrangle as arising in Cold Spring on the slope of

FIGURE 30. *Gila bicolor obesa*, from Humboldt River system, and a well differentiated race from Diamond Valley, Nevada. A. Humboldt River, near Lovelock (Location G2); UMMZ 124873, no. 11; considered topotypic; female, 108 mm. B. Bishop Creek (G4); UMMZ 141523, no. 24; male, 76.3 mm. C. Same field collection; no. 3; female, 114 mm. D. Sulphur Spring, Diamond Valley (G6); UMMZ 124927, no. 31; female, 82.5 mm.

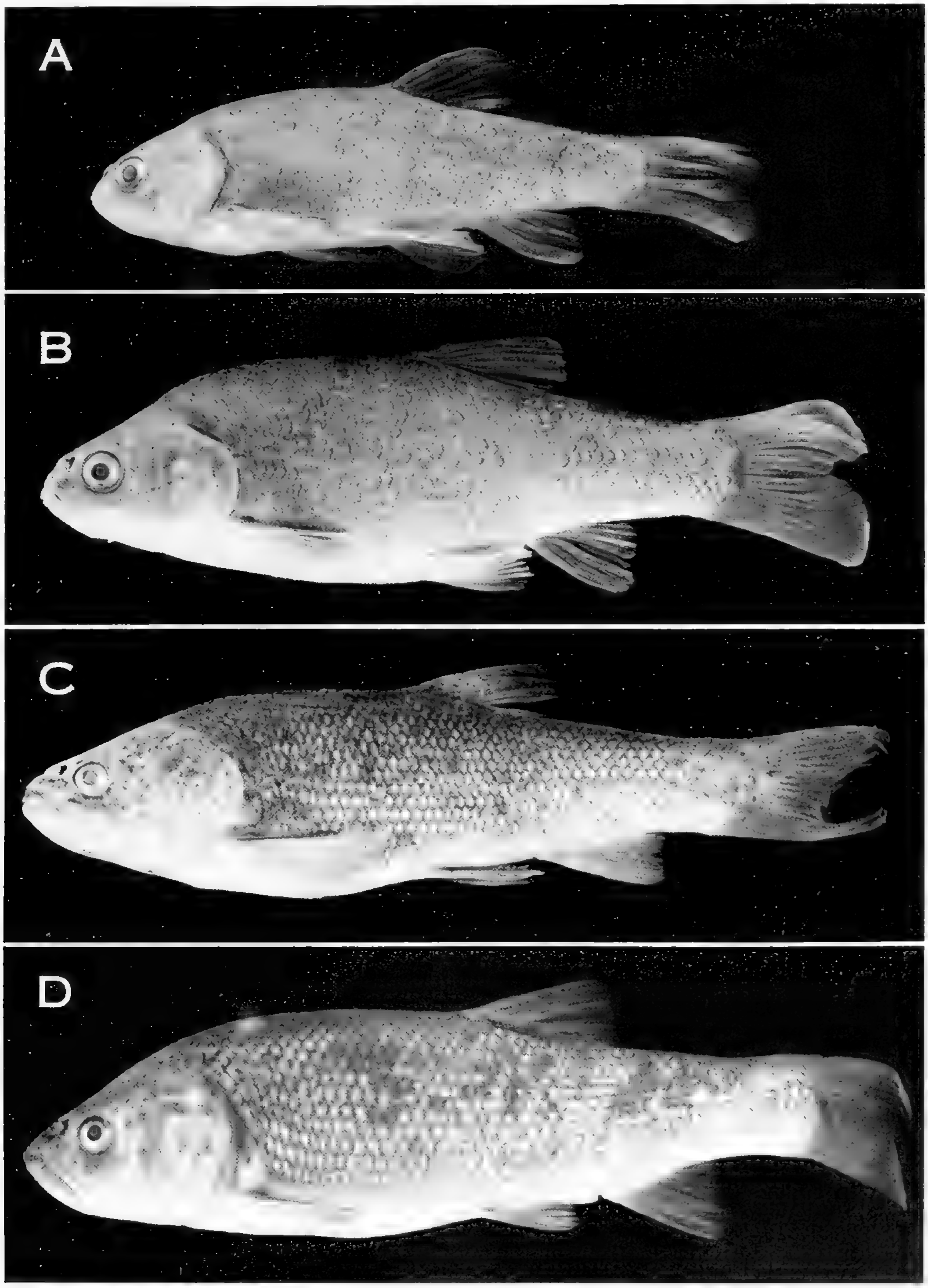


FIGURE 31. *Gila bicolor*: two subspecies from Newark Valley, Nevada. A. *G. b. newarkensis*, near Diamond Peak (Location G7); UMMZ 188893, no. 10; holotype, male, 68.0 mm. B. *G. b. newarkensis*, same field collection: UMMZ 132185, no. 8; paratype, female, 82.2 mm. C. *G. b. euchila*, Fish Creek Springs (G10); UMMZ 124939, no. 4; paratype, male, 114 mm. D. *G. b. euchila*, same field collection; UMMZ 124938; holotype, female, 141 mm.

Diamond Mountains, near the east base. It is mapped as being diverted into an irrigation ditch. The apparent lack of native fish in this little stream, as well as in the few other spring-fed rills that reach the floor of Newark Valley, is probably attributable to the flash floods that occasionally denude canyon streams in the land of rare but torrential waterflow.

It seems obvious that this subspecies was derived from *Gila bicolor obesa* of the Humboldt River system, or its immediate ancestor. Its distinctiveness is concordant with the evidence that the isolation dates from an earlier than the latest pluvial time (pp. 22–25).

Description and Comparisons.

Holotype, UMMZ 188893, a nuptial male 68.0 mm. in standard length (fig. 31A). Paratypes, UMMZ 132185, all other known specimens (226, 25–97 mm. long) from same Location (G7, data given above), including the adult female, 82.2 mm. long, that is illustrated (fig. 31B).

This subspecies is compared primarily with typical *Gila bicolor obesa*, as represented by populations of the Humboldt River system, and with the aberrant races, also referred to *G. b. obesa*, that inhabit Diamond Valley. Those drainage basins lie adjacent to Newark Valley. *Gila b. newarkensis* is compared with *G. b. euchila* of the Fish Creek Valley division of the basin of pluvial Lake Newark in the account of that subspecies. The other isolated form treated as a distinct subspecies, *G. b. isolata* of the drainage basin of pluvial Lake Clover, is compared later with *G. b. newarkensis*.

Size. *Gila bicolor newarkensis* is of medium to rather small size. The largest specimen in each of the two main collections measures 97 (G7) and 67 (G8) mm.

Coloration. The general color tone is darker and more uniform over the body than in the populations referred to *G. b. obesa*, not closely approaching the bicolored pattern of that subspecies. The coloration seems to enhance the turgid body form. Characteristically, the dark pigmentation of the sides is less uniform than in the other forms, because the melanophores are thickly and broadly concentrated around the margins of the scale pockets, leaving the rounded central area of the pockets largely clear, usually to form rather conspicuous stripes along the horizontal scale rows (figs. 31A,B). This pattern is usually most conspicuous ventrally. In some forms referred to *G. b. obesa*, sparser black pigment tends to margin the scale pockets (p. 151), less conspicuously, in a thinner, more diamond-shaped pattern, without forming definite horizontal streaks. The dark pigment extends farther down the sides than in even the upstream populations of *G. b. obesa* (fig. 30B,C), usually more or less completely rounding the caudal peduncle ventrally and reaching to a narrow midventral light wedge on the belly. The underlying dark lateral band is evident in small specimens, but seems to fade at a smaller size than it does in *G. b. obesa*. The basicaudal spot is replaced by a thin blackish streak along the curving posterior border of the squamation (in some young, the spot is weakly evident). This blackish streak may be confined to a vertical submedian position, or may extend farther, curving around the dorsal and ventral lobes of the squamation. As noted above (p. 152), the basicaudal spot tends to become minute or diffuse upstream in *G. b. obesa*, but not to form a streak. The fins are all darkened.

Life colors. The fish at Location G7 were described as follows, and those at G8 were noted as having the same color. Relatively uniform olive-green above to silvery below. Some have a very strong wash of pinkish-brassy, a yellow pectoral axil, and coppery-red-brown lower fins (whitish in others).

Form. The head and body are strongly turgid, rounded in all aspects. The contrast with fish from Sulphur Spring in Diamond Valley is sharpest, because the muzzle is much more broadly rounded, in both dorsal and lateral view, and the mouth is usually lower, more curved, and

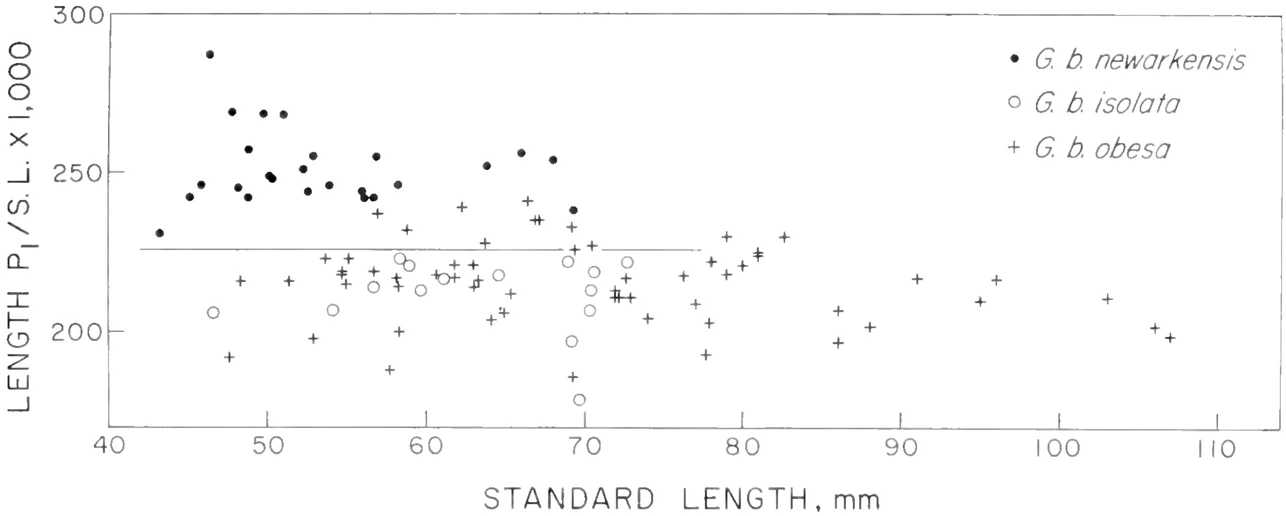


FIGURE 32. Usual distinction of *Gila bicolor newarkensis* from *G. b. isolata* and *G. b. obesa* in length of pectoral fin of males. The *G. b. obesa* material came from Bishop Creek (G4) and from Humboldt River near Lovelock (G2) and Carlin (G3).

less oblique, becoming more nearly horizontal forward; the mandible is slightly included at its front tip. The nuchal region is more humped, and the dorsal contour is scarcely elevated at front of dorsal fin. On the average these distinctions also hold when *G. b. newarkensis* is compared with the other populations referred to *G. b. obesa*. The fins are rounded, without any falcation, thus contrasting somewhat with even the upstream and Diamond Valley populations referred to *G. b. obesa*.

LATERAL-LINE SYSTEM. In half-grown fish the lateral line is sometimes more or less interrupted posteriorly, but in adults is nearly or quite complete.

In both main series of *G. b. newarkensis*, and in *G. b. euchila*, unlike all other populations of the species studied for this report, the supratemporal canal (table 26) is definitely and characteristically more often complete than incomplete —apparent evidence of the common origin of all the Newark populations.

MORPHOMETRY (table 27). On the average, and generally with limited overlap, *G. b. newarkensis* (as also *G. b. euchila*) differs from the forms referred to *G. b. obesa* as follows: the predorsal length is greater (confirming the trend toward greater development of anterior parts in isolated spring forms); the distance between pelvic insertion and anal origin is shorter; and the body, with some exceptions, the caudal peduncle (especially at Moores Ranch), and the head average deeper. The mouth, as indicated by the mandible length, is similar in size to that of *G. b. obesa*, and averages smaller than that of either *G. b. euchila* or *G. b. isolata* (table 27, figs. 34, 37).

The lengths of the pectoral and pelvic fins are about as usual in females of *G. b. newarkensis* and *G. b. euchila*, but in the males these fins, especially the pectoral, are unusually large (table 27, fig. 32), larger than in the other populations except that from Sulphur Spring.

SEXUAL DIMORPHISM AND NUPTIAL CHARACTERS. Apparently to a greater extent than is usual the dorsal fin is more posterior in females than in males, and in this subspecies (and also *G. b. euchila* and the Sulphur Spring population of *G. b. obesa*) the fins, especially the pectoral, are unusually large in males but are of about usual size

TABLE 27. *Proportional measurements, in permillage of standard length, for representative series of* Gila bicolor *in certain basins in Nevada. For each entry there is given the range, below this the mean, and, for the standard length and for items based on fewer specimens, the number of specimens (as a subscript).* *(Table continued on next three pages.)*

Subspecies	*Gila bicolor obesa*					*newarkensis*		*euchila*	*isolata*
Pluvial lake system	Lahontan			Diamond		Newark		Newark	Clover
Locality	Humboldt R. nr. Lovelock	Humboldt R. nr. Carlin	Bishop Creek	Birch Ranch	Sulphur Spring	Near Diamond Pk.	Moores Ranch	Fish Creek Springs	Independence Valley
Standard length									
Smaller ♀♀	52–94	45–98	45–95	55–81	53–86	47–97	49–67	49–98	51–91
	74_{23}	61_{20}	71_{15}	66_{10}	67_{20}	63_{19}	55_{15}	74_{25}	68_{15}
Larger ♀♀	108–115	100–105	101–137	—	—	—	—	101–143	—
	112_{6}	103_{2}	111_{8}	—	—	—	—	124_{13}	—
Smaller ♂♂	53–73	48–73	48–76	47–61	46–70	50–69	43–54	45–73	47–73
	63_{15}	63_{12}	61_{15}	53_{11}	59_{13}	58_{11}	49_{11}	59_{16}	63_{15}
Larger ♂♂	79–96	74–107	—	—	75–87	—	—	77–114	—
	83_{6}	82_{12}	—	—	80_{6}	—	—	91_{5}	—
Predorsal length									
Smaller ♀♀	521–562	534–567	529–580	532–559	530–570	543–602	555–610	565–621	560–593
	539	549	558	551	554	572	581	584	577
Larger ♀♀	548–567	539–541	544–590	—	—	—	—	561–613	—
	558	540	569	—	—	—	—	590	—
Smaller ♂♂	516–545	525–557	525–569	520–541	522–574	545–588	545–579	550–596	560–610
	533	542	547	532	542	569	563	575	578
Larger ♂♂	518–540	533–570	—	—	515–556	—	—	559–599	—
	527	546	—	—	536	—	—	579	—
Anal to caudal									
Smaller ♀♀	276–322	291–320	289–323	283–326	277–320	285–333	289–317	249–311	251–304
	300	306	309	305	295	310	300	288	288
Larger ♀♀	285–310	297–305	280–326	—	—	—	—	265–313	—
	296	301	306	—	—	—	—	285	—
Smaller ♂♂	291–335	292–329	300–341	306–336	287–324	309–345	300–337	286–330	282–313
	314	310	324	321	305	323	316	307	302
Larger ♂♂	294–328	292–320	—	—	288–321	—	—	290–315	—
	309	303	—	—	306	—	—	301	—
Pelvic to anal									
Smaller ♀♀	179–208	165–205	174–219	180–208	173–206	155–185	158–193	152–187	161–201
	192	184_{19}	195	197	190	170	172	170	185
Larger ♀♀	177–194	186–196	177–214	—	—	—	—	165–188	—
	184	191	196	—	—	—	—	175	—
Smaller ♂♂	177–219	166–204	173–202	166–207	170–207	158–185	155–192	160–191	163–216
	191	187	184	185	189	172	161	171	184
Larger ♂♂	179–204	167–197	—	—	183–194	—	—	163–180	—
	189	186	—	—	188	—	—	168	—
Body depth									
Smaller ♀♀	244–299	249–299	269–314	279–318	275–315	281–338	280–316	249–310	278–323
	270	268	287	300	296	304	298	283	303
Larger ♀♀	263–300	259–269	281–311	—	—	—	—	271–316	—
	276	264	299	—	—	—	—	292	—
Smaller ♂♂	246–274	249–282	261–313	265–304	243–306	291–329	277–304	263–302	284–329
	263	265	284	287	279	307	288	282	309
Larger ♂♂	265–293	258–287	—	—	277–324	—	—	267–311	—
	279	274	—	—	302	—	—	294	—

TABLE 27. CONTINUED.

Subspecies	*Gila bicolor obesa*					*newarkensis*		*euchila*	*isolata*
Pluvial lake system	Lahontan			Diamond		Newark		Newark	Clover
Locality	Humboldt R. nr. Lovelock	Humboldt R. nr. Carlin	Bishop Creek	Birch Ranch	Sulphur Spring	Near Diamond Pk.	Moores Ranch	Fish Creek Springs	Independence Valley
Peduncle depth									
Smaller ♀♀	111–133 123	107–131 119	112–135 126	118–133 125	117–133 125	120–145 131	135–150 142	120–142 131	119–149 135
Larger ♀♀	114–132 120	119–125 122	120–132 127	— —	— —	— —	— —	118–141 128	— —
Smaller ♂♂	120–135 126	105–129 121	118–135 130	117–138 130	115–135 124	132–148 138	134–157 145	123–148 136	135–153 142
Larger ♂♂	119–130 124	115–132 123	— —	— —	121–137 130	— —	— —	120–138 132	— —
Head length									
Smaller ♀♀	275–312 295	285–314 298	282–329 299	290–301 296	288–328 315	277–309 294	283–317 297	307–348 323	295–333 312
Larger ♀♀	282–299 292	284–298 291	271–319 298	— —	— —	— —	— —	294–337 316	— —
Smaller ♂♂	276–306 288	285–308 293	286–315 299	281–304 290	294–322 307	271–306 296	272–300 291	300–341 318	292–319 308
Larger ♂♂	282–300 289	275–305 292	— —	— —	283–317 302	— —	— —	308–324 313	— —
Head depth									
Smaller ♀♀	183–199 191	185–211 196	194–222 204	199–207 203	200–223 213	203–223 211	210–225 217	203–237 220	208–226 217
Larger ♀♀	184–199 192	187–194 191	190–218 203	— —	— —	— —	— —	212–232 224	— —
Smaller ♂♂	178–196 189	190–202 196	185–222 205	192–211 200	191–213 204	201–236 217	208–228 217	213–234 223	207–228 218
Larger ♂♂	186–197 191	185–203 193	— —	— —	188–214 202	— —	— —	212–237 226	— —
Head width									
Smaller ♀♀	139–163 149	138–163 148	150–175 161	153–171 158	157–191 170	151–163 157	151–167 159	155–195 171	152–180 168
Larger ♀♀	146–160 153	146–151 149	153–181 168	— —	— —	— —	— —	167–194 182	— —
Smaller ♂♂	132–149 142	139–157 147	146–168 157	137–165 154	149–176 159	146–171 158	150–167 159	156–178 166	156–186 169
Larger ♂♂	137–150 145	133–161 148	— —	— —	149–168 159	— —	— —	159–195 174	— —
Snout length									
Smaller ♀♀	68–85 79	72–89 78	74–91 83	79–86 82	79–100 84	75–86 80	79–101 87	76–103 92	77–96 88
Larger ♀♀	78–85 81	76–76 76	77–97 87	— —	— —	— —	— —	86–103 95	— —
Smaller ♂♂	69–85 77	71–83 76	77–89 85	74–87 81	75–87 79	74–83 78	77–87 83	84–102 92	77–90 86
Larger ♂♂	74–82 78	71–85 78	— —	— —	73–84 79	— —	— —	86–97 92	— —

TABLE 27. CONTINUED.

Subspecies	*Gila bicolor obesa*					*newarkensis*		*euchila*	*isolata*
Pluvial lake system	Lahontan			Diamond		Newark		Newark	Clover
Locality	Humboldt R. nr. Lovelock	Humboldt R. nr. Carlin	Bishop Creek	Birch Ranch	Sulphur Spring	Near Diamond Pk.	Moores Ranch	Fish Creek Springs	Independence Valley
Orbit length									
Smaller ♀♀	60–85 70	59–88 76	58–76 66	67–75 71	59–84 75	60–83 69	67–78 73	55–80 67	54–76 65
Larger ♀♀	56–58 57	58–58 58	46–60 52	— —	— —	— —	— —	49–59 53	— —
Smaller ♂♂	68–82 74	67–89 74	65–76 71	67–85 75	74–81 78	64–80 72	70–81 76	64–86 75	61–74 67
Larger ♂♂	61–68 65	58–68 63	— —	— —	63–71 67	— —	— —	51–70 63	— —
Upper-jaw length									
Smaller ♀♀	74–91 81	65–88 79	76–91 84	77–87 81	69–95 81	69–87 79	70–89 80	85–103 93	84–98 91
Larger ♀♀	78–86 81	79–81 80	75–94 87	— —	— —	— —	— —	84–104 96	— —
Smaller ♂♂	74–85 78	71–85 79	77–91 84	73–86 80	64–86 79	71–89 77	73–89 81	73–99 89	83–99 89
Larger ♂♂	75–81 77	75–88 81	— —	— —	73–85 79	— —	— —	86–97 91	— —
Mandible length									
Smaller ♀♀	98–120 108	98–120 107	94–111 104	100–112 107	103–123 114	92–109 103	95–112 104	107–125 116	105–120 114
Larger ♀♀	104–117 109	101–105 103	94–118 108	— —	— —	— —	— —	107–122 114	— —
Smaller ♂♂	99–110 105	96–112 106	96–108 103	98–110 103	100–111 107	90–106 100	94–109 103	105–119 113	105–119 112
Larger ♂♂	97–110 102	100–111 106	— —	— —	100–113 106	— —	— —	105–120 113	— —
Interorbital width									
Smaller ♀♀	89–108 97	86–106 97	94–112 102	93–102 96	93–113 108	89–104 96	96–114 104	100–112 105	91–107 100
Larger ♀♀	91–102 97	95–96 95	95–105 101	— —	— —	— —	— —	96–105 100	— —
Smaller ♂♂	85–102 94	89–111 98	94–106 101	91–105 99	88–103 97	84–99 92	98–122 108	96–116 106	94–108 100
Larger ♂♂	87–96 91	81–99 93	— —	— —	91–102 96	— —	— —	96–106 101	— —
Suborbital width									
Smaller ♀♀	34–43 38	32–42 37	32–47 40	34–43 38	34–50 44	35–43 39	37–50 42	43–57 48	37–46 42
Larger ♀♀	36–44 40	41–41 41	40–46 43	— —	— —	— —	— —	45–53 49	— —
Smaller ♂♂	31–40 35	33–42 37	34–44 39	32–47 38	31–43 38	33–45 39	36–52 42	44–53 48	38–44 41
Larger ♂♂	36–39 38	37–43 39	—	—	38–49 44	— —	— —	41–56 47	— —

TABLE 27. CONTINUED.

Subspecies	*Gila bicolor obesa*					*newarkensis*		*euchila*	*isolata*
Pluvial lake system	Lahontan			Diamond		Newark		Newark	Clover
Locality	Humboldt R. nr. Lovelock	Humboldt R. nr. Carlin	Bishop Creek	Birch Ranch	Sulphur Spring	Near Diamond Pk.	Moores Ranch	Fish Creek Springs	Independence Valley
Depressed dorsal									
Smaller ♀♀	222–258	205–264	202–238	220–264	235–286	212–252	210–242	205–248	198–249
	243	234_{13}	220	246_{7}	259_{19}	236	227	223_{21}	232
Larger ♀♀	212–238	206–227	194–227	—	—	—	—	199–220	—
	228	217	211	—	—	—	—	209	—
Smaller ♂♂	241–283	222–248	210–256	245–270	245–279	233–271	232–287	230–273	218–249
	255	236_{11}	236	257_{10}	262	257	251_{12}	248	237
Larger ♂♂	227–249	219–238	—	—	249–269	—	—	212–243	—
	237	228	—	—	257	—	—	229	—
Caudal length									
Smaller ♀♀	263–295	244–271	222–287	270–281	241–311	225–275	249–283	236–273	245–269
	280_{5}	261_{3}	251	275_{2}	276_{17}	247_{17}	265	253_{18}	260_{12}
Larger ♀♀	253–264	217	217–243	—	—	—	—	215–257	—
	258_{3}	217_{1}	235_{7}	—	—	—	—	239_{11}	—
Smaller ♂♂	266–317	260–269	234–286	267–273	262–288	241–290	255–300	248–292	251–278
	288_{4}	265_{2}	257	270_{2}	278_{7}	258_{4}	277_{10}	261_{10}	265_{17}
Larger ♂♂	261–270	258–265	—	—	258–284	—	—	260–265	—
	264_{3}	261_{3}	—	—	272_{3}	—	—	263_{4}	—
Pectoral length									
Smaller ♀♀	185–221	173–200	154–188	184–212	197–236	172–204	174–201	167–197	168–200
	201	189_{17}	175	199	216	185	189	187	183
Larger ♀♀	191–206	169–197	167–185	—	—	—	—	168–196	—
	198	183	174	—	—	—	—	183	—
Smaller ♂♂	198–241	204–237	186–232	199–242	217–252	238–268	231–287	207–281	179–223
	223	215	209	225	234	250	252	242	212
Larger ♂♂	217–230	197–230	—	—	208–253	—	—	204–235	—
	223	209	—	—	234	—	—	219	—
Pelvic length									
Smaller ♀♀	158–198	159–188	147–165	169–198	178–208	148–175	145–191	151–179	152–170
	182	170_{19}	160	181	193_{10}	163	164	164	160
Larger ♀♀	175–183	157–171	153–178	—	—	—	—	150–170	—
	178	164	163	—	—	—	—	160	—
Smaller ♂♂	176–208	171–190	164–193	180–211	196–213	172–199	168–197	164–206	152–176
	190	179	176	195	202	189	183	184	166
Larger ♂♂	184–201	164–186	—	—	193–208	—	—	177–200	—
	191	177	—	—	202	—	—	187	—

TABLE 28. *Sexual dimorphism in predorsal and fin lengths in populations of* Gila bicolor *in certain basins in Nevada, expressed as excess for males over females in mean values in permillage of standard length.*[1]

Subspecies / Pluvial lake system / Locality	Predorsal length		Dorsal fin		Caudal fin		Pectoral fin		Pelvic fin	
	Small fish	Large fish	Small fish	Large fish	Small fish	Large fish	Small fish	Large fish	Small fish	Large fish
Gila bicolor obesa										
Lake Lahontan										
Near Lovelock (15/23; 6/6)[2]	−6	−31	12	9	8	6	22	25	8	13
Near Carlin (12/20; 12/2)	−7	6	2	1	4	44[3]	26	26	9	13
Bishop Creek (15/15; —)	−11	—	16	—	6	—	34	—	16	—
Lake Diamond										
Birch Ranch (11/10; —)	−13	—	13	—	−5	—	26	—	14	—
Sulphur Spring (13/20; —)	−8	—	3	—	2	—	18	—	9	—
Gila bicolor newarkensis										
Lake Newark										
Near Diamond Peak (11/19; —)	−5	—	21	—	11	—	65	—	26	—
Moores Ranch (14/15; —)	−6	—	24	—	12	—	63	—	19	—
Gila bicolor euchila										
Lake Newark										
Fish Creek Springs (16/25; 5/13)	−15	−33	25	20	8	24	55	36	20	27
Gila bicolor isolata										
Lake Clover										
Independence Valley (15/15; —)	−5	—	5	—	5	—	29	—	6	—

[1] Based on values in table 27.
[2] The numbers in parentheses for each Location represent females and males, respectively, first for the smaller fish (in the size classes of 45–99 mm. for females and 43–73 mm. for males, including one fish 76 mm. long from Bishop Creek) and then for the larger adults (100–143 mm. for females, and 74–114 mm. for males).
[3] Only one female measured; other tallies for the caudal fin are based on a reduced number of specimens, because this fin is often broken.

in females. The sexual dimorphism in the length of the fins is extreme (table 28; figs. 31A–D). In this respect, *G. b. newarkensis* is approximately matched only by its congener *G. b. euchila*.

The nuptial characters of the male holotype (fig. 31A) are characteristic of the whole species (p. 179). The tubercles are confined to the upper surface of the pectoral fin, where they are strongest on the second and third rays, moderately strong along the first ray, and weak on the fourth ray. They are uniserial throughout on the first ray and basally on the next three, branching once, with the inner branch very weak on the fourth ray. They are regularly aligned, one per articulation of the ray. Each organ is sharply pointed and is slightly hooked mesad. The outer ray is rather thickly padded and the following several rays are considerably thickened. The fin is rigidly expanded in the horizontal plane, with the median area arched upward.

FIN RAYS (tables 29, 30). The dorsal rays, as usual in the Nevada populations of *Gila bicolor*, seldom deviate in number from 8. The anal-ray count averages low, and is modally reduced to 7, in all the samples from the basin of pluvial Lake Newark (further evidence of consanguinity and of meristic reduction in isolated springs). The caudal rays range from 16–20 at the type Location. The pectoral rays average somewhat less at Location G7 (15.88) than at G8 (16.50) or in *G. b. euchila* (16.71). The pelvic rays are more markedly reduced in average number in all the samples from the basin of pluvial Lake Newark (means 8.10–8.66) than in the samples referred to *G. b. obesa* (9.09–9.49)—again con-

TABLE 29. *Number of rays in the vertical fins in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality	Dorsal rays						Anal rays						Caudal rays						
	7	8	9	10	No.	Ave.	6	7	8	9	No.	Ave.	16	17	18	19	20	No.	Ave.
Gila bicolor obesa																			
Lake Lahontan																			
Carson River[1]	—	35	—	—	35	8.00	—	7	27	1	35	7.83	—	1	1	23	—	25	18.88
Humboldt River																			
Near Lovelock	—	60	1	—	61	8.02	—	13	47	1	61	7.80	—	—	1	58	—	59	18.98
Near Carlin	1	46	2	—	49	8.02	1	20	28	—	49	7.55	—	—	2	36	5	43	19.07
Bishop Creek	1	19	—	—	20	7.95	1	12	36	—	49	7.71	—	1	—	19	—	20	18.90
Lake Diamond																			
Birch Ranch	2	50	—	—	52	7.96	1	10	40	—	51	7.76	—	—	1	23	—	24	18.96
Sulphur Spring	—	63	—	—	63	8.00	—	3	59	—	62	7.95	—	—	1	26	—	27	18.96
Gila bicolor newarkensis																			
Lake Newark																			
Near Diamond Peak	3	61	6	—	70	8.04	1	63	6	—	70	7.07	1	1	9	50	4	65	18.85
Moores Ranch	7	62	—	—	69	7.90	1	65	3	—	69	7.03	—	—	5	29	3	37	18.95
Warm Springs	1	8	1	—	10	8.00	—	8	2	—	10	7.20	—	—	1	9	—	10	18.90
Gila bicolor euchila																			
Lake Newark																			
Fish Creek Springs	—	66	3	1	70	8.07	1	52	16	—	69	7.22	—	—	1	37	—	38	18.97
Gila bicolor isolata																			
Lake Clover																			
Independence Valley	6	79	—	—	85	7.93	1	118	25	—	144	7.17	—	1	8	64	—	73	18.86

[1] Some introgression from *Gila bicolor pectinifer*.

TABLE 30. *Number of rays in the paired fins (both sides counted) in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies / Pluvial lake system / Locality	Pectoral rays									Pelvic rays							
	13	14	15	16	17	18	19	No.	Ave.	6	7	8	9	10	11	No.	Ave.
Gila bicolor obesa																	
Lake Lahontan																	
Carson River[1]	—	1	15	32	14	2	—	64	16.02	—	-	—	55	15	--	70	9.21
Humboldt River																	
Near Lovelock	—	—	13	63	38	2	1	117	16.27	—	—		71	67	–	138	9.49
Near Carlin	—	9	34	36	3	2	—	84	15.46	—	—	—	68	28		96	9.29
Bishop Creek	—	7	16	15	2	—	—	40	15.30	—	—	7	259	117	1	384	9.29
Lake Diamond																	
Birch Ranch	—	3	13	32	4	—	—	52	15.71	—	—	—	72	32	–	104	9.31
Sulphur Spring	—	2	26	21	3	—	—	52	15.48	—	—	—	114	9	1	124	9.09
Gila bicolor newarkensis																	
Lake Newark																	
Near Diamond Peak	—	8	25	55	22	3	—	113	15.88	—	—	55	80	2		137	8.61
Moores Ranch	—	—	5	27	32	—	2	66	16.50	1	1	105	31	—	–	138	8.20
Warm Springs	—	—	—	—	—	—	—	—	—	—	—	18	2		-	20	8.10
Gila bicolor euchila																	
Lake Newark																	
Fish Creek Springs	—	—	3	30	30	10	2	75	16.71	—	1	44	90	1		136	8.66
Gila bicolor isolata																	
Lake Clover																	
Independence Valley	1	—	10	40	41	12	—	104	16.50	—	3	313	76			392	8.19

[1] Some introgression from *Gila bicolor pectinifer*.

firming both consanguinity and the trend toward reduction in isolated spring habitats.

VERTEBRAE. The vertebral counts (table 31) average fewer in the populations from the Lake Newark system (38.39 to 39.07) than in those referred to *G. b. obesa* (39.14 to 39.86).

SCALE ROWS. Almost all of the 11 scale-row counts also average lower in the populations from the Lake Newark system than in those referred to *G. b. obesa* (table 32). This is particularly true of the scale counts around body and around peduncle. The means are 44.4–46.7 *vs.* 52.2–56.5 and 24.6–26.3 *vs.* 29.6–32.0, respectively. These data, as do those for vertebrae, confirm consanguinity and reduction in springs.

GILL-RAKERS. The rakers in *G. b. newarkensis* are outstandingly few (table 22), short (table 25; fig. 28C), soft, and swollen. The mean number is fewer than in *G. b. obesa*, though in this respect *G. b. newarkensis* is closely approached by the headwater population of Bishop Creek. More strikingly in form than in number, the rakers of *G. b. newarkensis*, at both Locations where a good collection was secured, contrast with those of *G. b. obesa*, as represented by approximate topotypes from the Humboldt River near Lovelock (Location G2). They are opaque in preservative and are so fleshy and thick that they generally are in contact at the base, despite the low number. In *G. b. obesa*, in strong contrast, the rakers are slender, translucent, bony, and generally separated at the base.

There is little overlap in gill-raker length between *G. b. newarkensis* (or *G. b. euchila*) and the populations from Diamond Valley that we refer to *G. b. obesa*. The raker-length measurements for typical *G. b. obesa* are definitely intermediate between the values for *G. b. newarkensis* and the Sulphur Spring population (table 25, fig. 28).

PHARYNGEAL TEETH. The teeth (table 23) are usually 5—4, occasionally 4—4, rarely 5—5 or 4—5.

DERIVATION OF NAME. This subspecies was named for Newark Valley and for pluvial Lake Newark.

FISH CREEK SPRINGS TUI CHUB

Gila bicolor euchila Hubbs and Miller.
(Figure 31C,D.)

Gila bicolor euchila HUBBS and MILLER, 1972, p. 103 (diagnosis).

This subspecies is almost surely restricted to the waters of Fish Creek Springs, in Fish Creek (Little Smoky) Valley, in the southeastern corner of Eureka County, central Nevada. This valley is merely the southwestern expansion of Newark Valley, the sump of pluvial Lake Newark (pp. 22–26).

Location G10.—**Fish Creek Springs** in the northwestern part of Fish Creek (Little Smoky) Valley (tributary in flood to Newark Valley), on the valley flat near its west end, between the 6,020-foot and 6,040-foot contours on the Pinto Summit and Bellevue Peak 15-minute quadrangles; in main ditch about 0.5 km. below junction of the two main spring-fed branches (this places location near center of Sec. 8, T. 16 N., R. 53 E., about 3.5 km. west of the Fish Creek Ranch houses); near southwest corner of Eureka County, Nevada (figs. 3, 8). Clear, somewhat bitter, very slightly sulphurous; fine shelly sand, mud, clay, etc.; moderate current; moderate growth of bulrushes, *Potamogeton* (broad- and fine-leafed), *Chara*, and *Utricularia*; 20° C. (air 27°). Hubbs family, August 17, 1938 (M38-134); UMMZ 124938–39 (517, 18–149 mm.); 15-foot seine with ¼-inch square mesh.

Location G10A.—Collection made close by in another ditch, to make sure that small fish seen here were not *Rhinichthys*. Clear water; soil bottom; slight current; dense *Potamogeton*, cf. *P. pectinatus*; 24° C. (air 28°). Hubbs family, August 17, 1938 (M38-135); UMMZ 124940 (26, 15–37 mm.); 6-foot woven-mesh seine.

Collection M38-134 was made in a ditch 2–4 m. wide and to nearly 1.0 m. deep. These fish, in conformity with their morphology, were mostly in mid-water, with few on the bottom. They were locally known as "whitefish," as well as "chubs," presumably because the original settler, Fentstermaker, whose grave near the springs is marked on the Bellevue Peak 15-minute Quadrangle, used

the term "*Weissfisch*" by which name the larger cyprinids of Europe are known to Germans.

Isador Sara, the rancher then operating Fish Creek Ranch, supplementing other local information (p. 25), indicated in 1938 that about four years previously, he had stocked Fish Creek Springs with rainbow trout (*Salmo gairdnerii*) and brook trout (*Salvelinus fontinalis*) that he had obtained at Roberts Creek Ranch. These grew remarkably fast, he said, and had pink flesh, but were not as agreeable to eat as the chubs. He thought that the trout had not reproduced and were probably no longer present. One of the springs, intermediate in the southern drainage ditch, was found by us to swarm with the chubs, some adult but mostly young and half-grown. It formed a spring pool, about 10 m. in diameter, which had a very deep center, largely choked with *Utricularia* containing great quantities of amnicolid snails, seemingly like some sampled in the ditch.

No indications were obtained, by inquiry or field reconnaissance, that any other waters in Fish Creek (Little Smoky) Valley contain native fish. The extent of flow in Fish Creek is discussed in an earlier section (pp. 25–26).

Despite the circumstance that Fish Creek Springs, the sole habitat of this subspecies, lies in the same pluvial drainage basin as Newark Valley, the home of *G. b. newarkensis*, we regard the two as subspecifically separable. Although at times of torrential floods Fish Creek actually debauches onto the playa of Newark Valley we think it is highly improbable that there has been any gene interchange for hundreds and probably for some thousands of years.

It seems highly probable that the common ancestor of *G. b. euchila* and *G. b. newarkensis* arose from *G. b. obesa* when pluvial Lake Newark drained into Huntington Creek, a tributary to pluvial Lake Lahontan by way of Humboldt River. The distinctiveness of *G. b. euchila* and *G. b. newarkensis* from *G. b. obesa* is consonant with the evidence (pp. 23–25) that the isolation of the Newark basin and of its chub fauna dates from earlier than very late pluvial time.

Description and Comparisons.

Holotype, UMMZ 124938, an adult female 141 mm. in standard length (fig. 31D). Paratypes 124939, all other specimens (516, 18–149 mm. long) from same collection (M38-134; data given above, under Location G10); including the largest male, 114 mm. long (fig. 31C). The young from Location G10A were not designated as paratypes.

Comparisons in the following description are almost entirely with *G. b. newarkensis*, because the two subspecies, of almost certain common origin, share many significant features, and because *G. b. newarkensis* is compared, above, with *G. b. obesa*.

Size. An outstanding feature of this subspecies is its large size. The largest specimen measures 149 mm. in standard length, and many exceed 100 mm., whereas the largest example of *G. b. newarkensis* is only 97 mm. long, and the next largest specimen among the many hundreds in all the populations of all forms treated in this report is a 137-mm. example of *G. b. obesa* from Bishop Creek. The distinction in bulk is even more striking than in length.

Coloration. One of the most impressive features that are shared with *G. b. newarkensis* is the color pattern, which is essentially the same in general darkness and in pattern, involving rows of light-centered scale pockets, the far-ventral extension of the dark color, the darkening of the lower fins (even more pronouncedly than in *G. b. newarkensis*), and the transformation of the basicaudal spot into a blackish lining of the curved terminal margin of the scaly area.

Life colors. The field notes indicate that, distinctively, the females are deep moss-green on the back, with darker scale borders that tend to converge backward. The sides are usually strongly mottled or speckled on individual scales, with considerable gilt on the lighter scales. Some cheek scales show blue reflections. The lower sides are olive, abruptly giving way to the white ventral surface. The lower fins are deep-olive,

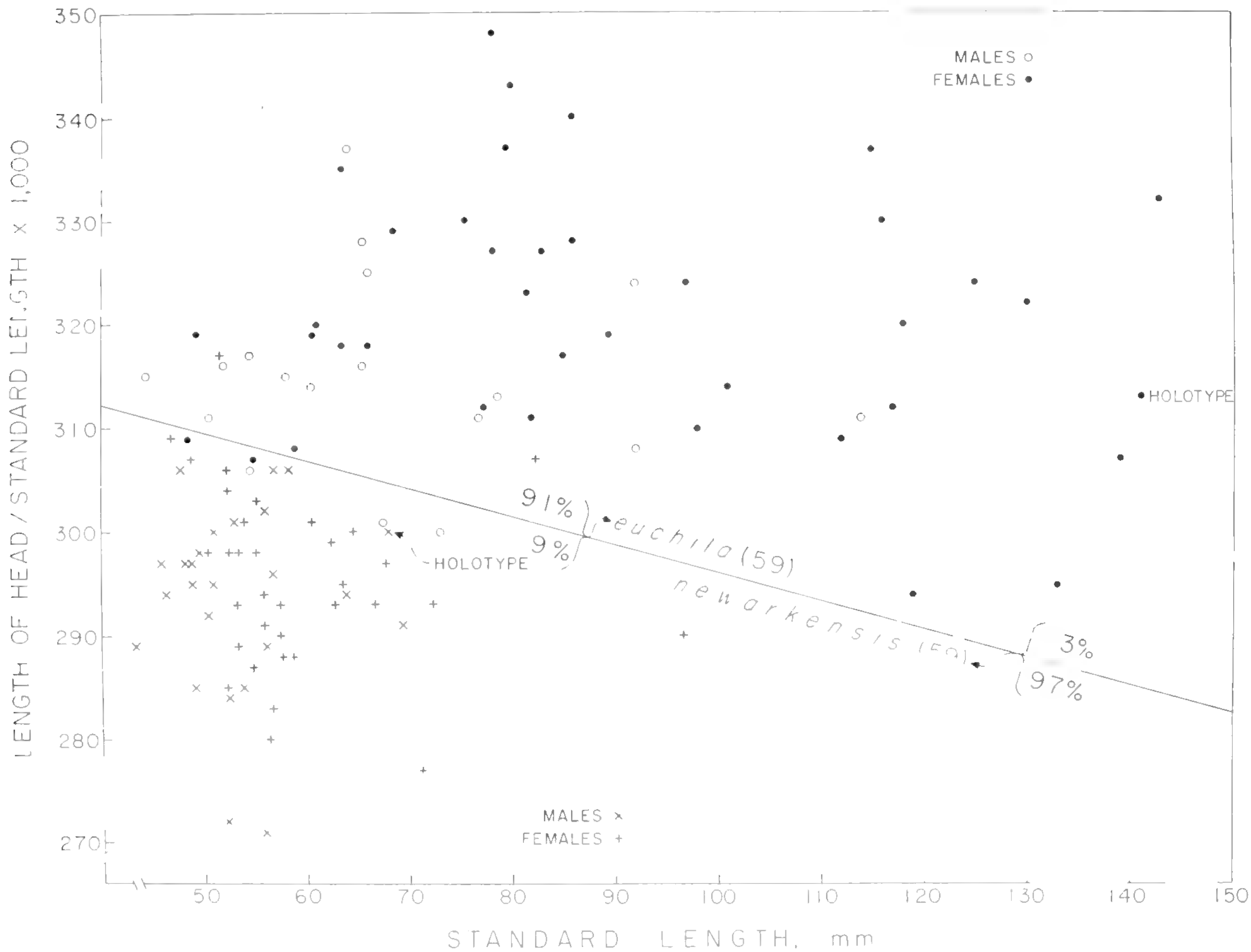


FIGURE 33. Usual distinction of *Gila bicolor euchila* and *G. b. newarkensis* in length of head of both sexes: showing percentages separable on basis of line maximizing differences (fitted by eye).

grading to blackish on the rays and to yellowish on the membranes, and have more or less indefinite whitish borders. The dorsal and caudal fins are very dark olive. There is often some orange in the axils of the paired fins.

Although in general similar in life colors, the adult males have much more gilt than the females on cheeks, opercles, and sides, and the gilt on the body is somewhat rosy. Blue reflections are rather strong on the lower sides, and the scale margins on the ventral area are orange-red, especially along the midline (this color feature is hardly evident on the low males). There is a considerable wash of lemon-orange on the dorsal and caudal fins. The axils of the paired fins are rather bright orange and this color is rather strong on the interradial membranes. The anal, pectoral, and pelvic rays are deep-olive. These fins are pale bluish near the border, especially toward the posterior angle.

The unusually bright colors observed in the field, on August 17, take on added significance on the finding that not a single nuptial male is included in the collection of 543 specimens, and that none of the females seem to be gravid.

FORM. The body contours are typically much less turgid than in *G. b. newarkensis* and the head is much more pointed in side view, with the tip much nearer the horizontal midline of head. The much straighter and less decurved anterodorsal

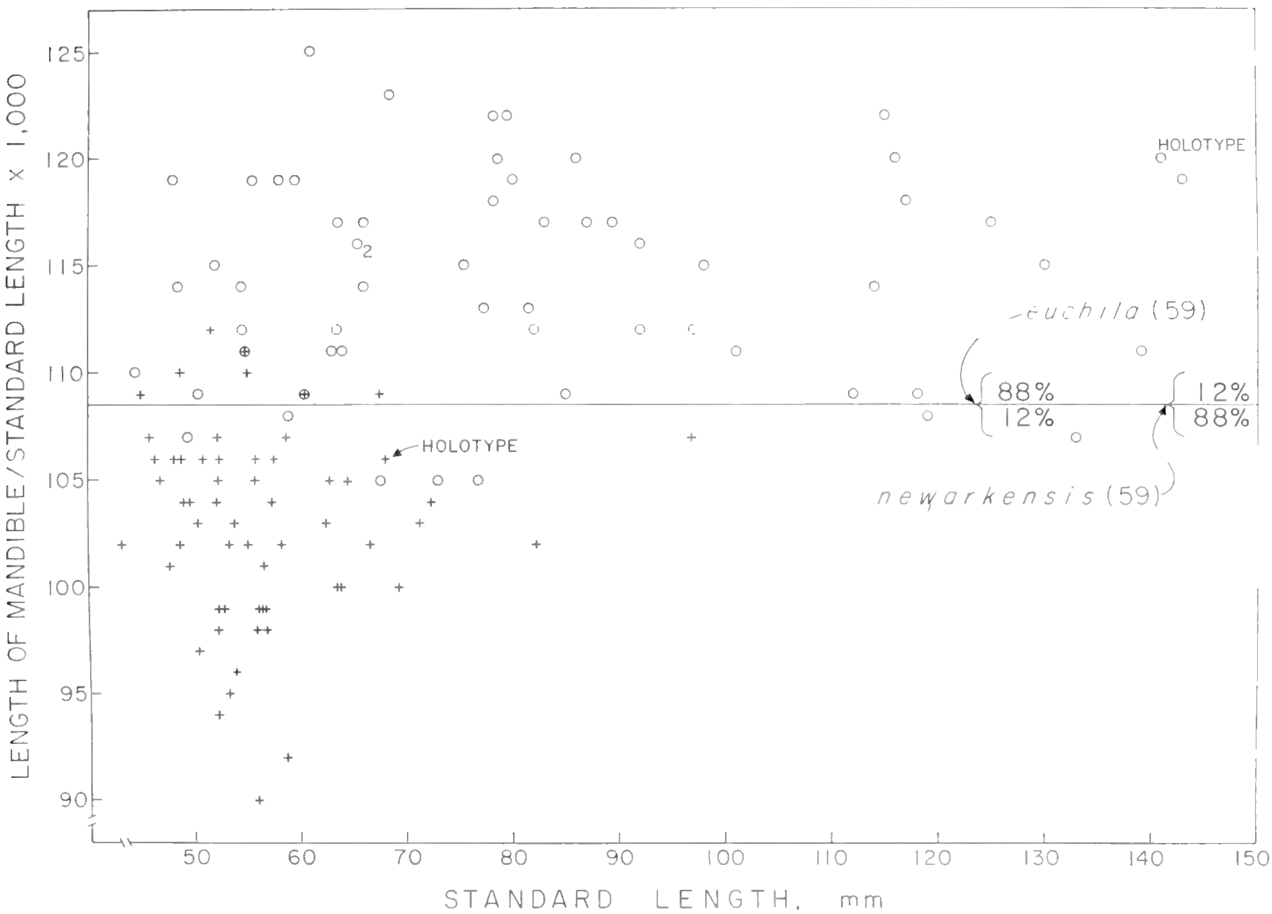


FIGURE 34. Usual distinction of *Gila bicolor euchila* and *G. b. newarkensis* in length of mandible of both sexes; showing percentages separable on basis of line maximizing differences (fitted by eye).

profile; the much larger head; the much larger, straighter, and more oblique mouth, with particularly massive lips and mandible; and the wide and flat suborbital and muzzle, combine to produce a very different effect, increasingly so in the large fish, but still obvious at like sizes. The impression given by these features, and by observations mentioned above, is that *G. b. euchila* is a midwater feeder, whereas *G. b. newarkensis* lives more on the bottom.

Despite its massive size (fig. 31C,D), the mandible, as in *G. b. newarkensis*, is slightly included within the front tip of the upper lip.

The fins are hardly falcate, but less rounded than in *G. b. newarkensis*.

LATERAL-LINE SYSTEM. In adults, the lateral line on the body is complete or nearly so when the scales are undamaged.

As in *G. b. newarkensis*, in contrast with all the other forms studied for this report, the supratemporal canal is much more often complete than incomplete (table 26).

MORPHOMETRY. The trend for isolated spring-inhabiting populations to have the dorsal fin set farther back than usual is carried in this subspecies to an extreme, among all the populations included in this study—slightly farther back than in *G. b. newarkensis*, but much farther, generally with little overlap, than in the other subspecies here treated (table 27). The distance from anal origin to caudal base averages proportionately shorter than in *G. b. newarkensis* and less than in the

other subspecies (except about the same as in *G. b. isolata*). The distance from pelvic insertion to anal origin is also low, as in *G. b. newarkensis.*

Because the anal-to-caudal and pelvic-to-anal proportions are both low, it was assumed that the distance from pelvic insertion to caudal origin might provide a quickly usable character. The pelvic-to-caudal dimension, measured with dividers on about 30 specimens of each Location, was stepped forward to see how far it reaches. In the several populations the dimension reached to any point specified below:

G. b. obesa

- G1. Carson River near Fallon: from rear part to front part of snout.
- G2 and G3. Humboldt River near Lovelock and near Carlin: from front edge of pupil almost to tip of snout.
- G4. Bishop Creek: from rear of pupil almost to tip of snout.
- G5. Birch Ranch, Diamond Valley: from front part of eye nearly to middle of snout, usually to front margin of eye.
- G6. Sulphur Spring, Diamond Valley: from rear edge of pupil to rear part of snout, usually to front part of eye.

G. b. newarkensis

- G7 and G8. Near Diamond Peak and at Moores Ranch, Newark Valley: from rear part of eye to slightly in front of eye, usually to about middle of eye.

G. b. euchila

- G10. Fish Creek Springs, Fish Creek Valley: from more than an eye's length behind eye to middle, rarely front edge of eye, usually to slightly before rear margin of eye.

G. b. isolata

- G11. Warm Springs, Independence Valley: from rear margin to just before front margin of eye, usually to near middle of eye.

The proportional measurements (table 27) verify the impression that in *G. b. euchila*, typically, the head, snout, upper jaw, mandible, and preorbital are distinctively large. In these proportions it contrasts sharply with *G. b. newarkensis* and is rather closely approached only by the otherwise very different Sulphur Spring population (G6, which is referred to *G. b obesa*). The sharpness of the distinction in length of head and length of mandible becomes particularly obvious by graphical presentation (figs. 33, 34). When the entries for the two subspecies are separated by a line seemingly maximizing the differences (approximately paralleling the trend of negative allometry for the head proportions and the essential isometry for the mandible proportions), the separation for the head proportion is 91 percent for *G. b. euchila* and 97 percent for *G. b. newarkensis*, and for the mandible 88 percent for each subspecies. Since neither form shows signs of stunting or abnormalities of growth, it appears highly probable that the differences in proportions are of basic significance.

The lengths of the pectoral and pelvic fins are about usual in females of *G. b. euchila* and *G. b. newarkensis*, but in males the paired fins, especially the pectoral, are larger than in the other populations, except that from Sulphur Spring in Diamond Valley.

SEXUAL DIMORPHISM. Sexual dimorphism in position of the dorsal fin and in length of fins (table 28) is extremely high, approximating that for *G. b. newarkensis* and far exceeding that for any of the other subspecies (another sign of consanguinity). As noted above, not a single male among the many collected was in nuptial condition on August 17. This circumstance, and the finding of large numbers of young, indicates spring or early summer spawning.

FIN RAYS (tables 29, 30). Dorsal rays 8 to 10, normally 8. Anal rays usually 7, as in some other spring-inhabiting subspecies of *Gila bicolor*, including *G. b. isolata* and all three populations of *G. b. newarkensis*. Pectoral rays 15–19, usually 16 or 17, averaging 16.71 (slightly higher than in any other population studied for this report). Pelvic rays 7–10, averaging 8.66; lower than in any population here referred to *G. b. obesa*, barely higher than in the type series of *G. b. newarkensis*, modally 9 as in that series, but significantly higher than in the two other populations of *G. b. newarkensis* and in *G. b. isolata*.

TABLE 31. *Number of vertebrae in populations of* Gila bicolor *in certain basins in Nevada.*

Subspecies Pluvial lake system Locality	Frequencies[1] 37	38	39	40	41	42	No.	Mean
Gila bicolor obesa								
Lake Lahontan								
Carson R.	—	—	3	10	1	—	14	39.86
Humboldt R.								
Near Lovelock	1	1	7	5	—	—	14	39.14
Near Carlin	—	—	7	8	2	—	17	39.71
Bishop Creek	—	1	10	12	—	1	24	39.58
Lake Diamond								
Birch Ranch	—	—	4	15	—	—	19	39.79
Sulphur Spring	—	—	4	12	—	—	16	39.75
Gila bicolor newarkensis								
Lake Newark								
Near Diamond Peak	2	7	6	1	—	—	16	38.39
Moores Ranch	—	3	7	4	—	—	14	39.07
Warm Springs	1	1	6	1	—	—	9	38.78
Gila bicolor euchila								
Lake Newark								
Fish Creek Springs	1	7	4	2	—	—	14	38.50
Gila bicolor isolata								
Lake Clover								
Independence Valley	2	19	9	—	—	—	30	38.23

[1] Including hypural complex as one vertebra and including the four comprising the Weberian apparatus.

VERTEBRAE (table 31). The vertebral average, 38.50, is slightly lower than in any of the populations here referred to *G. b. obesa*, within the range of variation for the populations of *G. b. newarkensis*, and slightly higher than in *G. b. isolata*.

SCALE ROWS. The counts of scale rows (table 32) in this subspecies and in *G. b. newarkensis* are similar, and average for all 11 categories lower than in any of the populations referred to *G. b. obesa* (except that the predorsal count is the same as in the Diamond Valley populations). For most of the categories there is little or no overlap; for some, the two forms of the Lake Newark drainage basin approximately correspond with or approach *G. b. isolata*; in other categories, the counts average lower.

GILL-RAKERS. The gill-rakers (table 22, fig. 29), as in *G. b. newarkensis*, average somewhat fewer than in the populations of Diamond Valley referred to *G. b. obesa* and in the headwater populations of that subspecies, and definitely lower than in downstream populations of *G. b. obesa*. The range (10–14) and the mean (11.77) slightly exceed the values for *G. b. isolata*.

In length (table 25, fig. 29) and in form the rakers in *G. b. euchila* (Location 10) are less consistently extreme than in *G. b. newarkensis* (Locations 7, 8), but usually are not so long, slender, and hard as they generally are in *G. b. obesa* (Locations 1–6). In length the overlap is extensive, when the comparison is made on the basis of permillages of the standard length, but this is in part attributable to the almost invariably larger head of *G. b. euchila*. In form, the rakers in *G. b. euchila* tend to be flask-shaped, thick, and fleshy basally, but to be more slender and less fleshy distally than in *G. b. newarkensis*.

PHARYNGEAL TEETH. In all 15 specimens checked, the teeth (table 23) number 5—4.

DERIVATION OF NAME. The subspecies name was derived by combining the prefix ευ, good or well, with χειλος, lip, in reference to the conspicuously enlarged mouth and fleshy lips. It is treated as adjectival, hence given feminine termination.

TABLE 32. *Number of scale rows in populations of* Gila bicolor *in certain basins in Nevada.*[1]

Subspecies Pluvial lake system Locality (No.)[2]	Lateral-line series	Pre-dorsal rows	Above lateral line	Below lateral line	Lateral line to pelvic	Around body: Above	Around body: Below	Around body: Total	Around peduncle: Above	Around peduncle: Below	Around peduncle: Total
Gila bicolor obesa											
Lake Lahontan											
Carson River (19)	52–64 57.3[3]	28–34 31.3	12–16 13.4	8–11 9.6	8–10 8.5	26–31 27.9	23–30 26.6	51–62 56.5	12–17 15.2	13–17 14.8	28–35 32.0
Humboldt River											
Near Lovelock (30)	49–61 54.7	24–32 27.4	11–14 12.3	7–10 8.6	6–9 7.3	24–29 26.6	22–30 24.5	49–61 53.0	13–16 14.7	13–16 14.1	28–34 30.8
Near Carlin (30)	52–62 56.2	22–34 28.8	12–14 13.0	8–10 8.9	7–9 7.7	25–30 27.6	23–31 26.2	51–63 55.8	14–16 15.0	12–17 14.8	29–35 31.8
Bishop Creek (20)	47–59 52.5[4]	23–31 27.7	11–14 12.6	8–10 8.8	6–9 7.6	23–28 26.1	23–28 25.3	48–58 53.5	12–16 14.2	12–15 13.4	26–32 29.6
Lake Diamond											
Birch Ranch (10–12)	51–56 53.4	25–31 27.1	12–14 13.3	8–10 9.1	7–8 7.8	25–28 26.6	23–26 24.3	50–55 52.8	14–15 14.7	13–15 13.9	29–32 30.6
Sulphur Spring (30)	50–59 53.4	24–30 27.0	12–14 13.1	8–10 9.1	6–8 7.3	25–28 26.5	21–26 23.7	48–55 52.2	14–16 14.7	13–15 13.9	29–33 30.7
Gila bicolor newarkensis											
Lake Newark											
Near Diamond Peak (30)	44–50 47.7	22–30 26.5	8–12 10.4	6–9 7.1	6–8 6.7	20–25 21.8	20–25 21.8	42–50 45.6	11–14 12.2	11–14 11.9	24–30 26.0
Moores Ranch (30)	44–53[5] 49.2	24–29 26.6	9–11 9.9	6–8 6.9	6–9 6.5	19–23 21.1	19–25 21.3	41–49 44.4	10–13 11.1	10–13 11.5	22–28 24.6
Gila bicolor euchila											
Lake Newark											
Fish Creek Springs (30)	42–53 47.3	23–32 27.0	9–11 10.1	6–8 7.1	5–8 6.6	19–26 22.2	19–26 22.5	40–54 46.7	9–15 12.5	9–14 11.8	20–30 26.3
Lake Clover											
Independence Valley (20)	43–53 48.1[4]	24–32 27.3[6]	10–13 12.1	7–9 7.7	6–8 7.0	22–26 24.6	22–28 25.1	47–56 51.7	10–15 12.6[6]	10–14 12.5[6]	24–29 26.6[6]

[1] For each, range and mean are given.
[2] Number of specimens, in parentheses, except as indicated by footnotes.
[3] 20 specimens.
[4] 30 specimens.
[5] Five specimens from Warm Springs in Newark Valley have 49–54 scales in lateral-line series, averaging 51.0.
[6] 19 specimens.

INDEPENDENCE VALLEY TUI CHUB

Gila bicolor isolata Hubbs and Miller.
(Figure 35A.B.)

Gila bicolor isolata HUBBS and MILLER, 1972, p. 103 (diagnosis).

This subspecies is almost certainly confined to Warm Springs, the only fish-inhabited water in Independence Valley, the eastern arm of the bed of ancient Lake Clover, in east-central Elko County, Nevada (pp. 29–32). Here, it occurs with a companion relict, *Rhinichthys osculus lethoporus* (pp. 134–140). *Gila* does not occur in Clover Valley, the western arm of the same lake bed, where two populations of *R. osculus* comprise another endemic subspecies, *R. o. oligoporus*. The locality for *Gila b. isolata* and *R. o. lethoporus* is marked G11 and R12 on figure 12.

Location G11.—Warm Springs of Independence Valley: described under Location R12 for *Rhinichthys osculus lethoporus* (p. 134).

First collection (August 25, 1965). UMMZ 186518 and 186906 (285, 25–97 mm.).

Second collection (April 3, 1966). CAS 24567 (61, 26–64 mm.), collected by Stephen Harold Berwick (aided by William Nisbet and Jeffrey Newman), was donated by Dr. Robert J. Behnke to the California Academy of Sciences. A 10-foot seine with ¼-inch square mesh was used in outlet flowage and main pond.

The second collector of this subspecies, Mr. Berwick, expanded a study of his material into a class report, which Dr. Behnke has made available. In this report Mr. Berwick treated the population as an undescribed subspecies and dealt with its habitat and with the systematics of the tui chubs in general, in correlation with the paleohydrography of the Great Basin.

Gila bicolor isolata abounds in the ramifying waters of this spring complex, and seems greatly to outnumber *Rhinichthys osculus lethoporus*, the associated relict endemic. The chub is more midwater in habitat than the dace, and is less inclined to take quick refuge in the dense vegetation. For some time no dace were recognized during the first collection. After a few were noticed, vigorous seining in the vegetation was required to obtain the series of 101 specimens. No dace were included in the second collection.

Field reconnaissance and repeated inquiries brought no indication that the cyprinids were introduced into the Warm Springs of Independence Valley, or that any fish occur anywhere else in that valley. The trenchantly distinctive characters of the local form of each of the species leave virtually no room for doubt that the populations are native.

DESCRIPTION AND COMPARISONS.

Holotype, UMMZ 186906, an adult female 85.8 mm. in standard length (fig. 35B), from first collection. Paratypes, all other known specimens, 25–97 mm., listed above, including, also from the first collection, the adult male, 64.6 mm. long, that is illustrated (fig. 35A).

The characters of the two endemic minnows and the physiographic evidence (pp. 29–32) indicate that both were derived from an ancestor that inhabited the adjacent headwaters of the Humboldt River, of the pluvial Lake Lahontan drainage basin. The connection presumably took place in the Pleistocene, but not during very late pluvial time. The ancestors were presumably *Gila bicolor obesa*, of a type very similar to the population sampled in Bishop Creek, and *Rhinichthys osculus robustus* (or very similar precursors).

The two endemic subspecies of Warm Springs in Independence Valley agree in being more or less dwarfed, and in being among the most sharply differentiated of the fishes that were derived through the disruption of their now endorheic basins from the Lahontan drainage system. The evidence is presented in the account of *Rhinichthys osculus lethoporus* (pp. 134–140).

Some osteological features of *G. b. isolata* are used as representative of the genus in the comparative account of the skeletal features of *Relictus* (pp. 182–193).


A
B
C
D

This well marked subspecies is compared with *G. b. obesa* and the two other subspecific isolates of *Gila bicolor* herein described, namely *G. b. newarkensis* and *G. b. euchila*, both in the drainage basin of pluvial Lake Newark.

SIZE. *Gila bicolor isolata*, like the other isolated spring forms other than *G. b. euchila*, is somewhat dwarfed. The largest male measures 73 mm. in standard length; the largest female, 91 mm. The other similarly dwarfed populations are those of Newark Valley (*G. b. newarkensis*) and those of Diamond Valley (aberrant races of *G. b. obesa*).

COLORATION. The general tone of the preserved specimens is variably dusky. The underlying axial dusky band is strong in the young and typically is somewhat more distinctly retained than usual in the adult. Individual blackened scales are more conspicuous than in most forms. The dark color extends onto the lower sides of the body, but a wider band is left unpigmented on the lower sides than is usual in *G. b. newarkensis* and *G. b. euchila*. In *G. b. isolata*, unlike those subspecies, the pigment almost never rounds the ventral surface of the caudal peduncle. However, almost all specimens of *G. b. isolata* have a highly distinctive black speck on the midventral line at the very origin of the lower procurrent caudal rays—a mark that is almost never developed in any of the other subspecies here considered. In some specimens, fine lines in a vertically elongated diamond-shaped pattern appear on the lower sides (a feature of the Diamond Valley populations referred to *G. b. obesa*). An occasional specimen shows the well aligned rounded light scale-pocket centers, such as are usually developed in *G. b. newarkensis* and *G. b. euchila*. The basicaudal black spot, about as in Humboldt upstream and Diamond Valley populations referred to *G. b. obesa*, is usually more or less evident, though much reduced in size and/or intensity. Some specimens bear a trace, generally weak, of a fine black line rounding the end of the squamation on the caudal base (a usual feature of *G. b. newarkensis* and *G. b. euchila*). An occasional specimen combines this streak and the basicaudal spot.

LIFE COLORS. The life colors were not noted in the field, and no bright pigmentation is recalled. This is probably a plainly colored form, and as such would seemingly contrast with *G. b. euchila* (pp. 169–170).

FORM. Generally the body is well rounded in cross section. The profile is little elevated at nape or front of dorsal. The snout is moderately pointed (less so than is usual in *G. b. euchila*). The anterodorsal profile is less rounded and decurved than it usually is in *G. b. newarkensis*. About as in *G. b. obesa*, contrasting with *G. b. newarkensis* and *G. b. euchila*, the front tips of mandible and upper lip are about even; the mandible varies from very slightly included to somewhat protruding, rather than being slightly to moderately included. In contrast with *G. b. newarkensis*, the mouth is usually nearly straight, and is sufficiently oblique to rise nearly to the lateral midline of the head, to about opposite lower edge or middle of pupil, instead of to opposite lower edge of pupil or lower part of eye below pupil. The straight, oblique, and large mouth suggests midwater feeding. In further contrast, particularly with *G. b. newarkensis*, the fins are rather pointed, though they are more often somewhat rounded than slightly falcate (the nearest trend toward falcation is shown by the anal fin).

LATERAL-LINE SYSTEM. The lateral line, even in the larger adults, is usually incomplete pos-

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FIGURE 35. Types of *Gila bicolor isolata* and *Relictus solitarius*. A. *Gila bicolor isolata*, Warm Springs, Independence Valley, Nevada (Location G11); UMMZ 186518, no. 23; paratype, male, 64.6 mm. B. *G. b. isolata*, same field collection; UMMZ 186906; holotype, female, 85.8 mm. C. *Relictus solitarius*, Kirkpatrick Ranch, Butte Valley, Nevada (Collection 7); UMMZ 186904; holotype, nuptial male, 60.3 mm. D. *R. solitarius*, same field collection; UMMZ 141518; paratype, female, 89.8 mm.

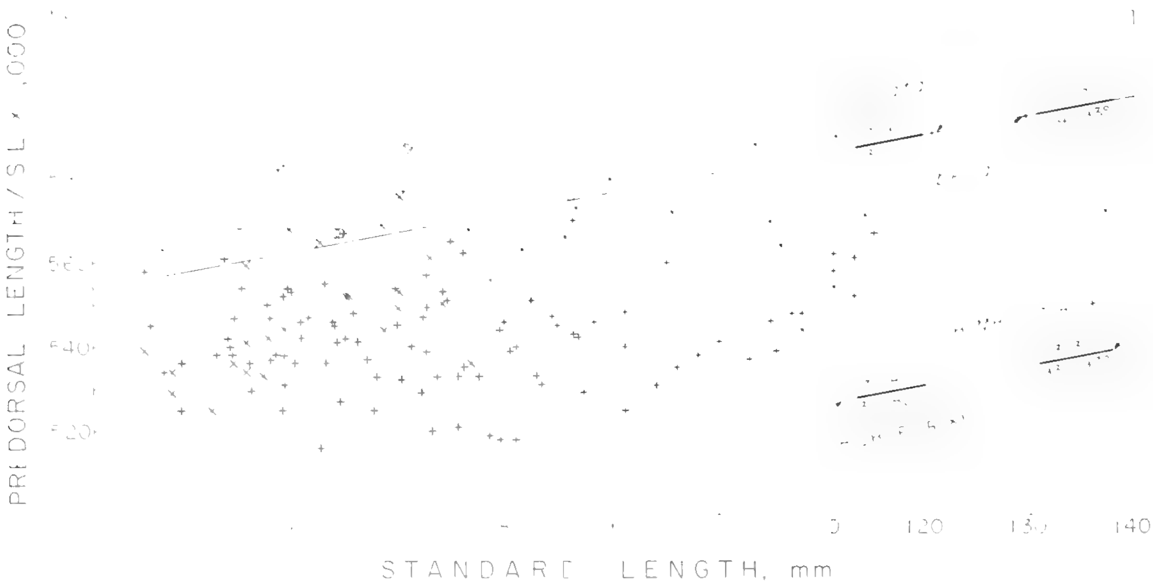


FIGURE 36. Usual distinction of *Gila bicolor isolata* from *G. b. obesa* in predorsal length, in Bishop Creek (G4) and in Humboldt River at Lovelock (G2) and Carlin (G3), combined and separated: showing percentage separable on basis of line maximizing differences (fitted by eye).

teriorly, lacking at least on the posterior part of the caudal peduncle, usually throughout that region, and sometimes farther forward, where it may be either lacking or interrupted. This is a common feature of western cyprinids that are restricted to isolated springs (p. 181), but the lateral line is not more than incipiently interrupted in any of the other subspecies of *G. bicolor* here considered.

Strangely, however, this is the only subspecies among those here treated in which the supratemporal canal is regularly complete (table 26). In this respect, *G. b. isolata* is approached by the subspecies of the Newark basin.

MORPHOMETRY. With very little overlap, the dorsal fin is farther back than in any of the other forms considered, except *G. b. newarkensis* and *G. b. euchila* (table 27). The backward position of the dorsal fin is one of the characteristics of western cyprinids that inhabit isolated springs. When the proportional values for predorsal length are plotted against standard length (fig. 36), and a line separating the entries for the two taxa is drawn approximately paralleling the allometric increase in this dimension, 90 percent of the specimens in the *G. b. isolata* sample are separated from 93 percent of the specimens from the Humboldt system, and the entries for the nonconforming specimens are not far beyond the line of separation. This is particularly striking when it is noted that the sexes are combined in the graph and it is recalled that females tend to have the more posterior position of the dorsal fin. It is further remarkable that such a high degree of distinction is obtained, despite the circumstances that the fish from Bishop Creek have on the average a more posterior dorsal than those from Humboldt River (of the 10 entries for *G. b. obesa* that lie just on the *G. b. isolata* side of the separating line, 7 are from Bishop Creek). The Humboldt River and Bishop Creek specimens are, respectively 97 and 82 percent separable from 90 percent of those representing *G. b. isolata*.

There are other average distinctions in morphometry. The distance from anal origin to caudal base is shorter on the average than in the other subspecies, including *G. b. newarkensis*, but is similar in this respect to *G. b. euchila*. Body and

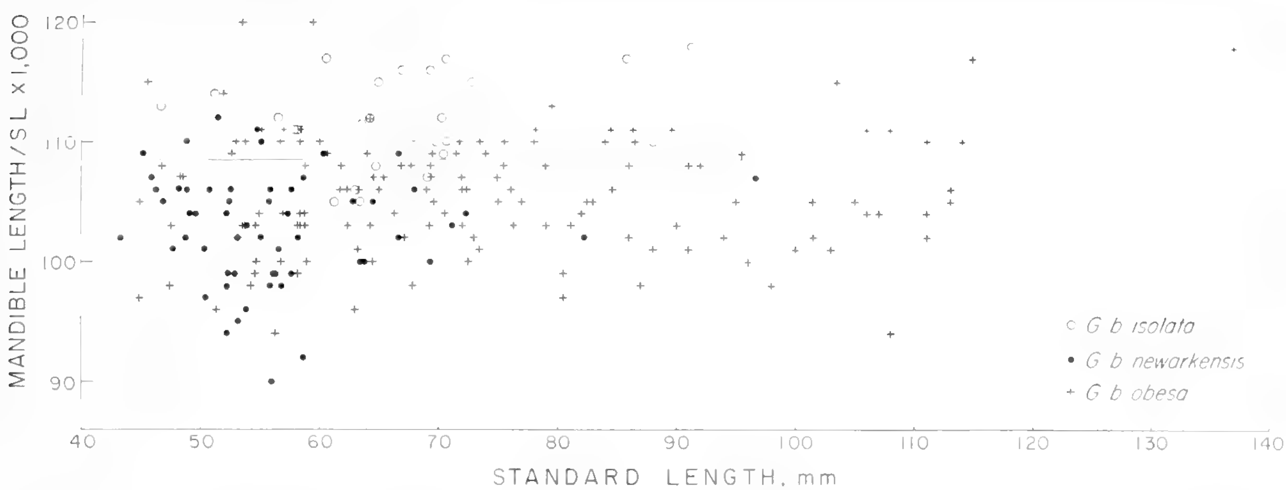


FIGURE 37. Usual distinction of *Gila bicolor isolata* from *G. b. newarkensis* and *G. b. obesa* in length of mandible. The *G. b. obesa* material came from Bishop Creek (G4) and from Humboldt River near Lovelock (G2) and Carlin (G3). The horizontal line (fitted by eye) separates 83 percent of the *G. b. isolata* entries from 88 percent of the *G. b. newarkensis* entries.

caudal peduncle average deeper than in most forms. The head averages a little smaller than in *G. b. euchila* and the Sulphur Spring population of *G. b. obesa*, but larger than in the other sets studied. The mandible averages about the same in length as in the Sulphur Spring population of *G. b. obesa* and in *G. b. euchila*, but larger than in any of the other forms herein reported upon (figure 37 compares the length of the mandible in *G. b. obesa*, *G. b. newarkensis*, and *G. b. isolata*). The length of the pectoral fin in males is almost always less than in *G. b. newarkensis* or *G. b. euchila*, about the same as in *G. b. obesa*.

SEXUAL DIMORPHISM AND NUPTIAL CHARACTERS. Sexual dimorphism (table 28) in the position of the dorsal fin (indicated by the predorsal length) is slight, and the difference between the sexes in the size of the dorsal, caudal, and pelvic fins is unusually slight. In respect to the size of the pectoral fin, the sexual dimorphism averages about as in *G. b. obesa*, and is much less than in *G. b. newarkensis* and in *G. b. euchila*.

The nuptial characters are typical of *Gila bicolor*. A small, obviously late maturing male 46.6 mm. long, in the first collection, of August 25, exhibits the typical nuptial tuberculation and the usual structural modification of the pectoral fin. The tubercles are strong on the first 3 rays and are arranged one per segment of the ray; each is a slender spine hooked basad and mesad. They are aligned in one row only on the outermost ray and branch once on the second and third rays. There are a few on the fourth ray, with the file not branching. The tubercles on the four rays vary from strongest on the second ray through intermediacy on the third and first rays to weakest on the fourth. The outer pectoral rays are considerably thickened. No tubercles are apparent on other fins, on the head, or on the body scales. Most of the adult males in the second collection, presumably yearlings taken closer to the normal breeding season (on June 18), are in nuptial condition. The tuberculation is similar, except that the spinelets extend, decreasing in strength, onto additional rays, to the seventh. The small size of the nuptial specimens suggests that the males first spawn as yearlings.

FIN RAYS (tables 29, 30). Dorsal rays number 8, rarely 7. As in *G. b. euchila* and in two of the three populations of *G. b. newarkensis*, anal rays are predominantly 7, rather than 8. Caudal rays deviate downward from 19 in 8 percent of

the specimens counted. Pectoral rays number, on the average, slightly on the high side. As also in two of the three populations of *G. b. newarkensis,* the pelvic-ray counts are predominantly reduced from 9 to 8.

VERTEBRAE. The average number of vertebrae (table 31) found for *G. b. isolata* (38.23) is slightly lower than for *G. b. newarkensis* and *G. b. euchila*, and definitely lower than in the populations referred to *G. b. obesa*. The modal number is 38, instead of 39 or 40.

SCALE ROWS. In correlation with the reduced number of vertebrae, the number of scales in the 11 rows counted is low (table 32). The mean number of scales in the lateral line (48.1) roughly corresponds with the means (47.3–49.2) found for *G. b. newarkensis* and *G. b. euchila*, respectively, and is definitely lower than the means (52.5–57.3) for the populations referred to *G. b. obesa*. The mean scale count around caudal peduncle yields similar differences (in the same sequence, 26.6 compared with 24.6–26.3 and contrasted with 29.6–32.0). The mean number of scale rows around the body (51.7) is higher than the means for *G. b. newarkensis* (44.4 and 45.6) and for *G. b. euchila* (46.7), and is more nearly in agreement with the means (51.0–56.5) for *G. b. obesa*. Means for other row series are intermediate between those for *G. b. newarkensis* and *G. b. euchila*, as compared with *G. b. obesa*.

GILL-RAKERS (table 22). The rakers in *G. b. isolata* average slightly fewer (11.14, with range of 8–14) than in *G. b. newarkensis* and *G. b. euchila* (11.75–12.23, with range of 9–15), and not much lower than in the Bishop Creek headwater population of *G. b. obesa* (12.61, with range of 10–15). There is only limited overlap on the counts for the Diamond Valley populations or on the counts for the other series of *G. b. obesa* considered.

In length (table 25) and form, the rakers of *G. b. isolata*, except for extreme variants, are essentially like those of typical *G. b. obesa* (p. 153), and contrast with the short, fleshy rakers of *G. b. euchila* and, more strikingly, with those of *G. b. newarkensis*. On the other side, the contrast is also great with the long, slender, and hard rakers of the populations, referred to *G. b. obesa*, that inhabit Diamond Valley, especially with the Sulphur Spring series.

PHARYNGEAL TEETH. All 13 specimens checked have the expected number of teeth, 5—4 (table 23).

DERIVATION OF NAME. The name *isolata*, of obvious significance, was derived from *insula* + *ato*, modified in spelling as in Italian, French, and English.

GENUS **RELICTUS** HUBBS AND MILLER

Relictus HUBBS and MILLER, 1972, p. 101 (diagnosis).

TYPE SPECIES. *Relictus solitarius* Hubbs and Miller.

Specimens of this cyprinid were first collected in 1934 and 1938, when, in the hope of determining whether the fish might indicate a Lahontan or a Bonneville derivation, we first sampled the fish life of the endorheic basins of Nevada that intervene between those drainage basins. Instead, we found in that area a unique fish in many respects unlike any occurring to the west or east (or to the north or south). In our treatment of the fish life of the Great Basin (Hubbs and Miller, 1948b, pp. 51–55), we mentioned this fish "as a type of dace that is so distinctive as probably to warrant generic separation from *Rhinichthys*," and, in discussing its limited distribution, we suggested that the basins it inhabits may be the remnant of an ancient, early pluvial drainage system. The only subsequent mention of the fish in the literature has been a very brief reference by La Rivers (1962, p. 86) to our 1948 treatment.

In reconsidering this distinctive minnow, we find considerable support for our long-felt opinion that it should be segregated in a distinct genus. Until we carried out this renewed study, our opinion was based on the indications that it does

not fit any of the recognized genera, and that it displays a distinctive combination of the characters that had generally been utilized to distinguish genera among western American cyprinids. In view of the tenuous nature of the long-used characters, which have been falling into some disrepute, and in view of the finding of some trenchant differences in skeletal structures among western minnows (Uyeno, 1960; Uyeno and Miller, 1965), we undertook, toward the elucidation of this and other problems, a comparative study of some bones of the cranium, upper and lower jaws, mandibular and hyoid arches, pectoral girdle, and fifth branchial arch. The number and morphology of the chromosomes has also been determined. This study has disclosed a character complex of distinctive features, which in our opinion confirm, even in this era of lumping, our long-held view that the relationships of this species are best portrayed by assigning it to a separate genus.

Relictus takes its place, along with *Moapa* and *Eremichthys* (Hubbs and Miller, 1948a), among the distinctive endemic relict fishes that occupy limited areas of spring water within the Great Basin. It is less extremely restricted in its distribution than those genera, for it is native throughout most of the basin-bottom springs of four valleys (pp. 196–226): Ruby and Butte valleys, within the connected pluvial drainages of lakes Franklin and Gale, and Goshute and Steptoe valleys, within the connected pluvial drainages of lakes Waring and Steptoe.

This type of dace provides an excellent example of the modification, in part degenerative, that characterizes fishes, particularly cyprinids, that are confined to isolated springs in the Great Basin and elsewhere (Hubbs, 1940, p. 201; 1941a; 1941b, p. 187; Hubbs and Miller, 1948b, pp. 51–52). These modifications include: a body form adapted to midwater swimming in quiet water, with more or less symmetrically curved dorsal and ventral contours of body and head; generally rather chubby, with deep caudal peduncle; a terminal and generally rather large mouth, fitted to engulf organisms living at various depths; small, weak, and rounded fins, adequate for limited locomotion in quiet water; reduction or obsolescence of the barbels, the lateral line, and other dermal sense organs, not critically needed in the absence of most enemies; scales tending to lose their orderly arrangement and wide imbrication, and, in correlation, tending to develop radii on all fields; (generally) dusky colors. The type of dace under treatment (fig. 35C,D) partakes of all these modifications.

Diagnosis

A cyprinid of moderate size (larger than *Rhinichthys*), with some distinctive osteological characters: dorsal crest of maxilla greatly expanded upward and backward; cleithrum slender; supraethmoid elongate, slender medially but notably expanded laterally at front (resembling that of *Rhinichthys*); urohyal long and narrow. Vertebrae 35–39. Pharyngeal arch moderately strong and heavy, but rather thin and somewhat lacy on the strongly expanded median section; not strongly elevated at the posterior end of the tooth row; without a flattened shelf on which a second tooth row might develop; teeth 4—4 (rarely 5—4 or 4—3). Gill-rakers small and few (7–12, usually 8–11, on first arch). Mouth oblique and terminal, completely lacking horny cutting edges; no frenum or barbel. Lateral line obsolescent, rarely extending to below origin of dorsal fin, commonly disrupted; total pores 3–29. Supratemporal canal seldom complete (only 4 of 76 specimens have the commissure closed), with usually 3 or 4 (0–5) pores in each lateral segment; preoperculomandibular pores 11–19; mandibular pores 3–8. Scales rather small (50–70 transverse rows), poorly imbricated and markedly irregular; each usually vertically oval, but sometimes becoming rectangular with age; with numerous radii on all fields (much as in *Rhinichthys* and some other western genera). Fins small and strongly rounded; the pelvic especially and uniquely paddlelike; dorsal and pelvic both dis-

placed backward, and both beginning at approximately the same vertical (as in the subgenus *Siphateles* of the genus *Gila* and in many species of the typical subgenus *Gila*); dorsal and pelvic rays typically 8, anal 7. Nuptial tubercles form a highly distinctive pattern (p. 221) on head: the largest uniserially line the infraorbital sensory canal and suborbital margin; large uniserial caducous cones (much stronger than in *Gila*) line the upper edge of the first pectoral ray; smaller cones, also strictly uniserial (not forking once as they do in *Rhinichthys*) occur along one to several following rays; in high males some tubercles develop along outer pelvic rays and along first anal rays. Head and body turgid. Coloration much as in *Siphateles*, rather even, and often with large melanophores on lower side; lacking the two lateral bands, the head stripe, the paired light spots at caudal base, and other features characteristic of *Rhinichthys* (pp. 104–105). Intestine forming a single, simple, compressed-S loop (type 1 of Kafuku, 1958, p. 56), as in *Rhinichthys* and many other American cyprinids.

Description

In this section we expand on the Diagnosis, particularly on the osteological characters, while largely avoiding repetition. Some additional description is presented in the species account. In the osteological treatment, we have stressed comparison with *Rhinichthys*, utilizing primarily skeletal material of *Rhinichthys osculus reliquus*, but with characters to a large degree confirmed by examination of skeletons of additional subspecies of *R. osculus* and of other species referred to the genus (*R. cataractae*, *R. falcatus*, and *R. atratulus*).

Skeletal characters. In the oro-mandibular region, the maxilla (fig. 38) proves to be one of the distinctive bones of *Relictus*. This paired dermal structure lies dorsolateral to the premaxilla and is partly covered laterally by the ventral part of the lachrymal, which overlies the entire dorsal crest of the maxilla. At its anterior end the maxilla is expanded and, projecting from it ventromesially, is the rodlike rostral process which, with the lateral plate, holds the anterior part just behind the ascending process of the premaxilla. The strongly elevated dorsal crest, lying midway in the length of the maxilla, is so greatly elongated as to occupy about one-half that length. Its shape varies from that shown, in which the leading edge slopes backward and the posterior border is strongly concave, to a form with an abruptly elevated leading edge and with the posterior border only slightly concave. In the considerable expansion of the dorsal crest *Relictus* is unmatched by any other genus of western minnows.

The premaxilla, also a paired dermal bone, is overlapped laterally by the maxilla, but is here drawn separately (fig. 38B). The anterodorsal part forms an ascending ramus or rostral process, which is directed toward the anterior end of the cranium, where it contacts the tiny rostral bone. The posteroventral end of the premaxilla overlies the slightly expanded posteroventral flange of the maxilla. The slender rostral process is tilted slightly forward at its dorsal end. The slender premaxilla tapers gently posteriorly. Its depth across the angle at the anterior end is greater than one-fourth the total length of the maxilla. Its shape is somewhat intermediate between that of *Gila bicolor* and that of *Rhinichthys osculus*.

The olfactory region of the cranium contains a bone, the supraethmoid (fig. 39B, SE), which, in combination with other features, is distinctive of *Relictus*, though it is very similar to that of *Rhinichthys*. The thin, horizontal, unpaired supraethmoid sutures posteriorly with the anteromedial parts of the frontals (F). Its anteroventral part is fused with the anterodorsal surface of the underlying ethmoid bone (E). The noteworthy feature of this bone in *Relictus* is its elongate and relatively narrow shape: the least width enters the total length about 5–8 times. Among western cyprinid genera, the supraethmoid of *Relictus* resembles closely only that of *Rhinichthys*, which

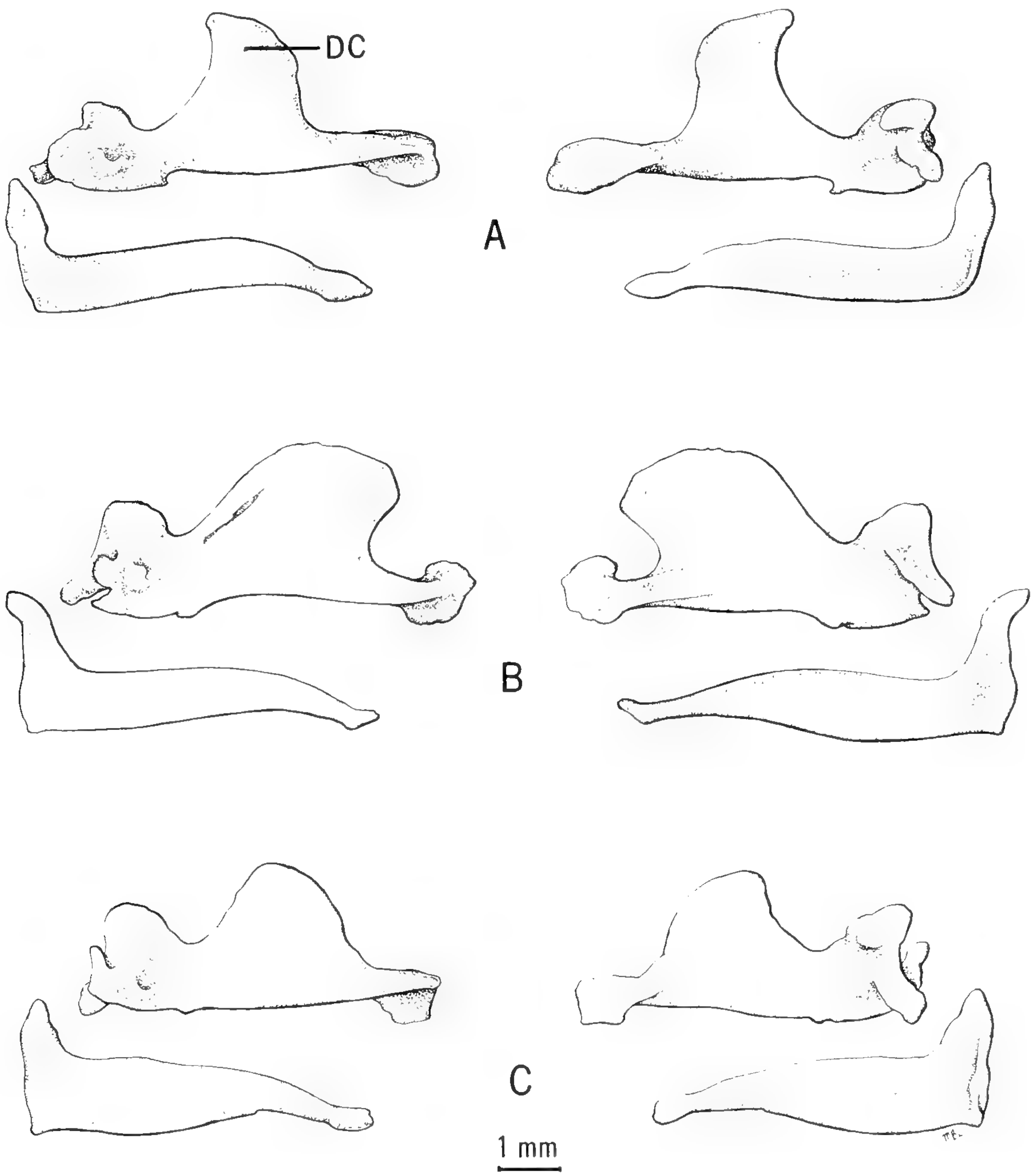


FIGURE 38. Lateral (left) and mesial (right) views of left maxillae and premaxillae of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (91 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ, 124907). DC, dorsal crest.

varies considerably in shape among the several species but is also elongate and is very to moderately narrow (checked in the five currently recognized species). As seen in dorsal view, the anterior end of the supraethmoid of *Relictus* is incised by a median notch, of variable width and depth, that more or less divides this region into two lobes, as described for the genus *Gila* and

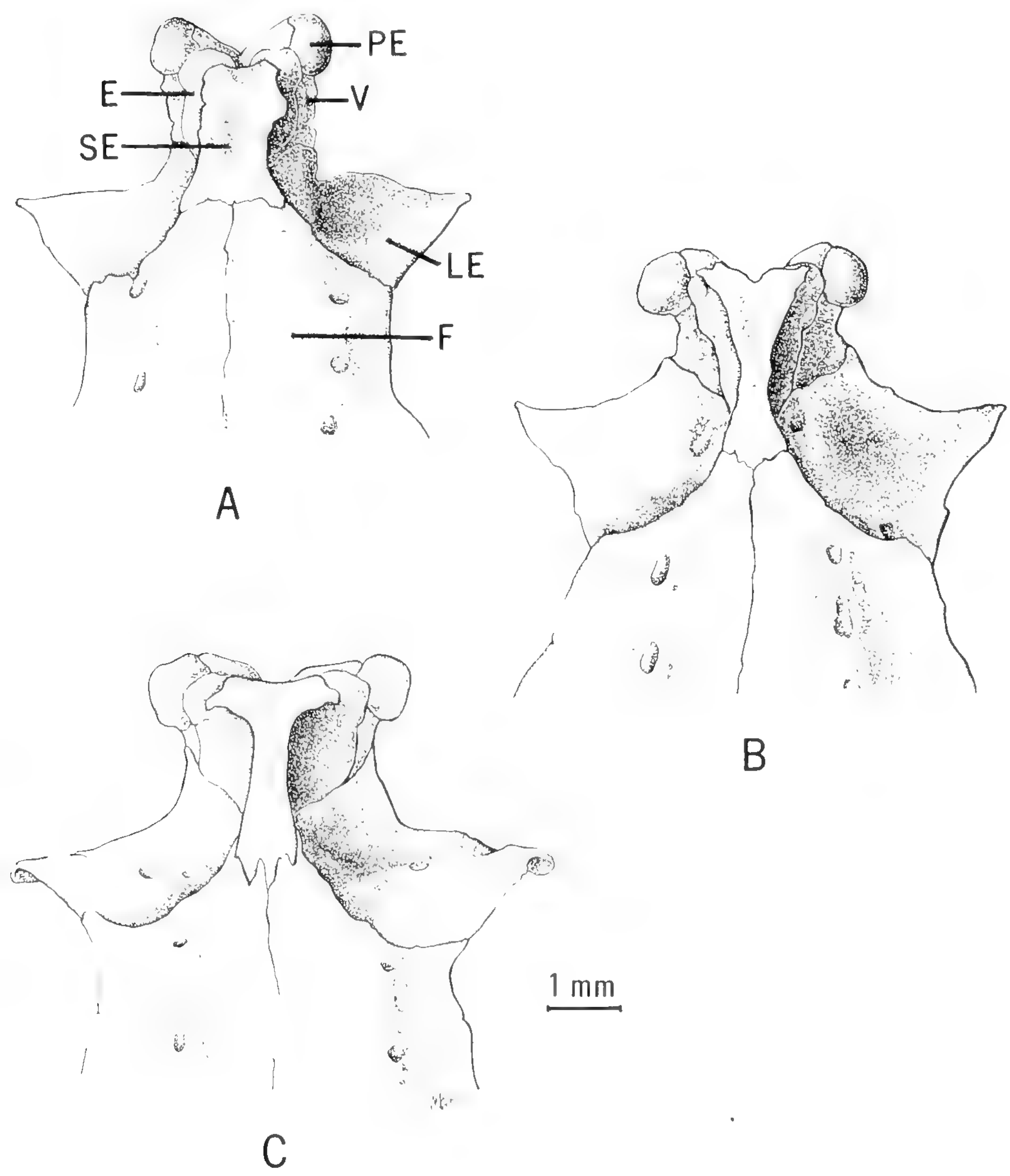


FIGURE 39. Anterior end of crania of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (88 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ 124907). E, ethmoid; F, frontal; LE, lateral ethmoid; PE, preethmoid; SE, supraethmoid; V, vomer.

its relatives (Uyeno, 1960). The shaft of the supraethmoid is slenderest medially, but expands notably forward (only slightly or hardly at all posteriorly). In all other western cyprinid genera, the supraethmoid is shorter and broader than it is in either *Rhinichthys* or *Relictus*.

One bone of the hyoid region, the hyomandibular, is illustrated for comparison of *Relictus* with *Gila* and *Rhinichthys* (fig. 40). This is a well developed paired cartilage bone that forms the posterior suspensory mechanism for the opercular apparatus, mandibular arch, hyoid arch, and branchial arches. It lies in front of and articulates posteriorly with the preopercle and opercle and dorsally with the hyomandibular fossa of the cranium. Its form often provides features of

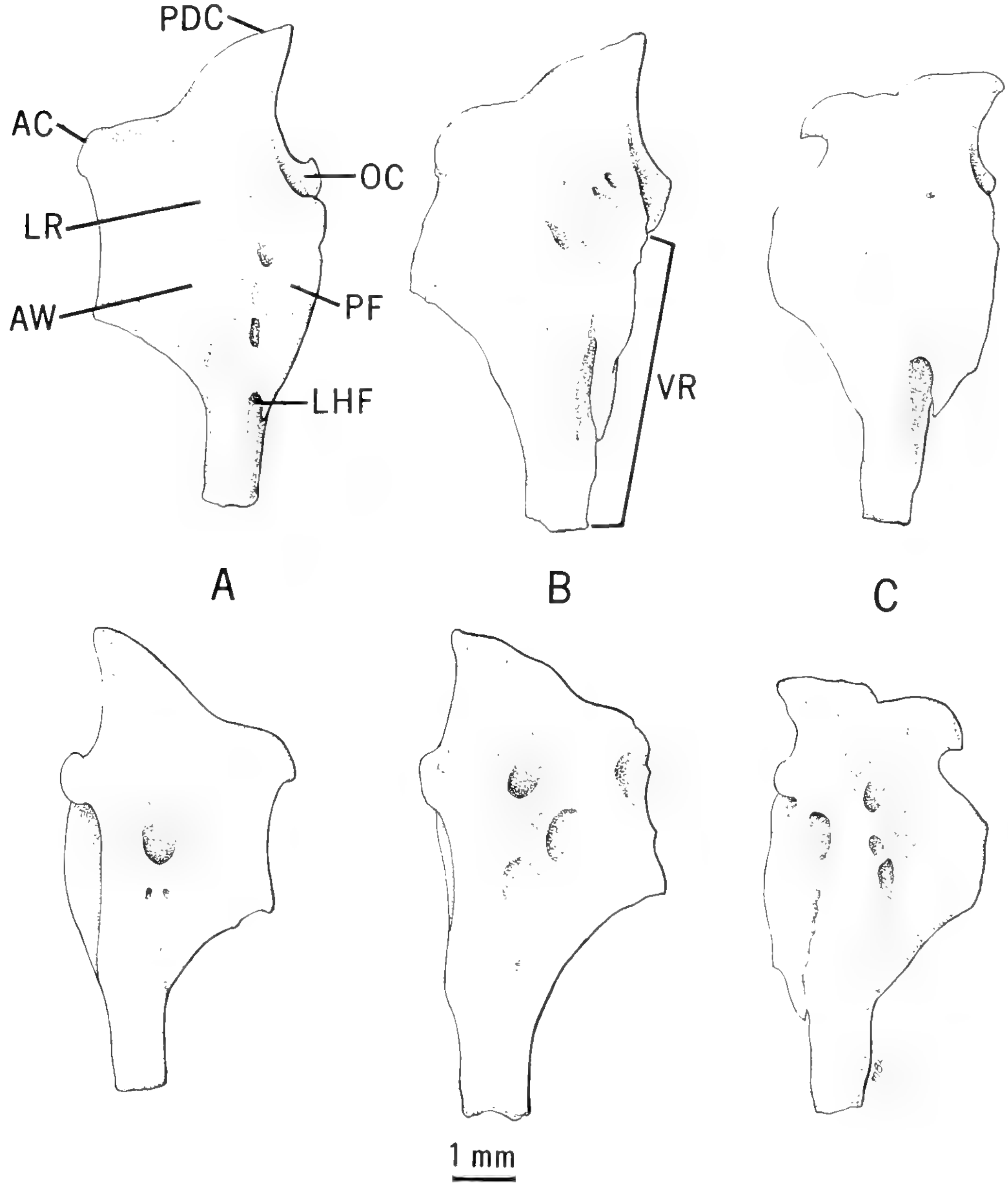


FIGURE 40. Lateral (above) and mesial (below) views of left hyomandibulars of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (88 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ 124907). AC, anterior condyle; AW, anterior wing; LHF, lateral hyomandibular foramen; LR, lateral ridge; OC, opercular condyle; PDC, posterodorsal condyle; PF, posterior flange; VR, ventral ramus, length.

taxonomic value at the species, or even the generic, level, as has been shown by Uyeno and Miller (1965, fig. 4), whose nomenclature of the parts of the bone is here adopted. In *Relictus*, the anterior wing is moderately to strongly developed. Its slightly convex anterior border extends from less than one-third to about one-half the distance down the ventral ramus. The dorsal edge, between the posterodorsal condyle (PDC) and the anterior condyle (AC), forms an angle

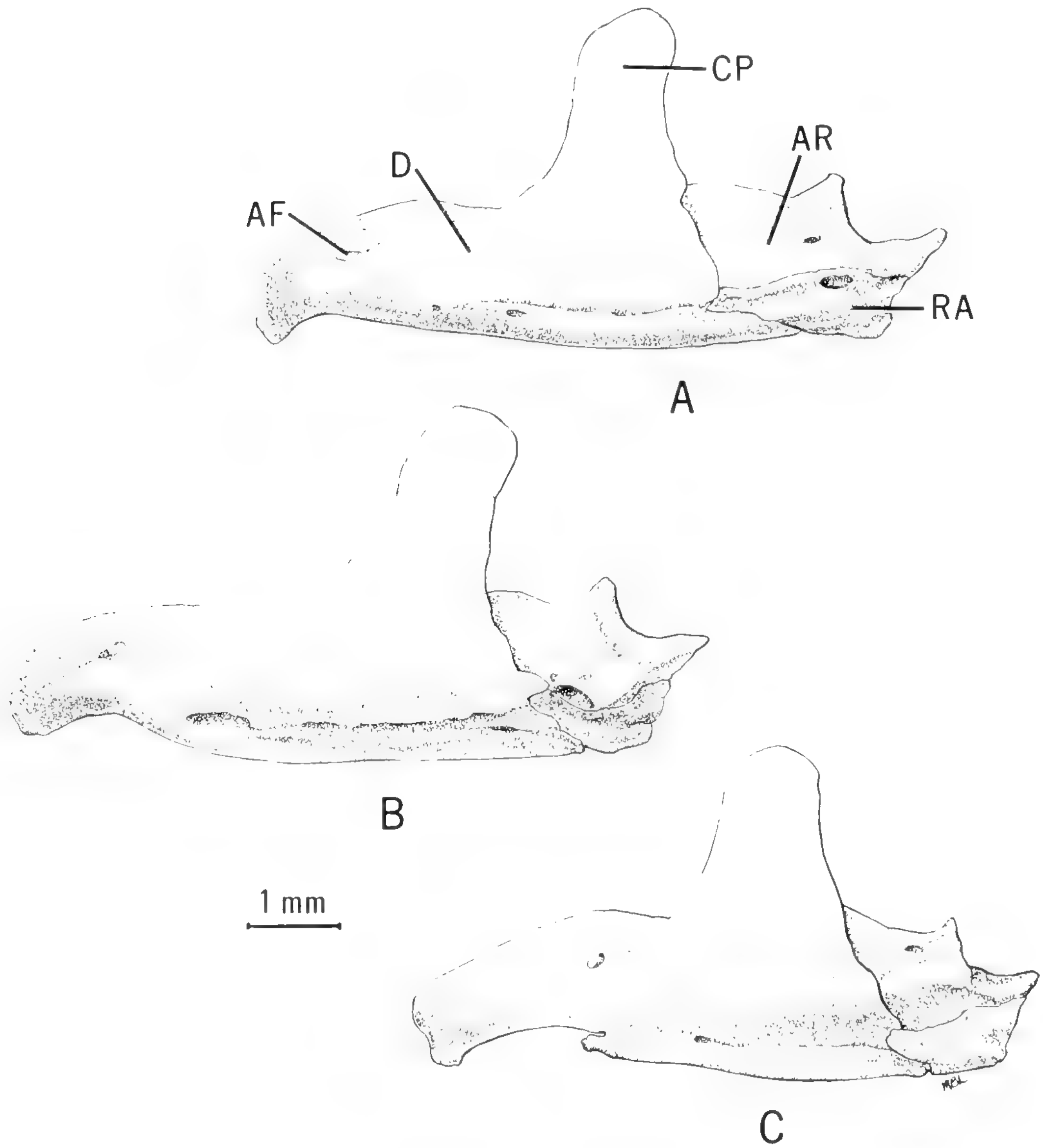


FIGURE 41. Lateral views of left lower jaws of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (91 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ 124907). AF, anterolateral foramen; AR, articular; CP, coronoid process; D, dentary; RA, retroarticular.

of about 60° with the vertical, as in *Gila*. The lateral hyomandibular foramen (LHF) is at the end of a canal roofed by very thin bone that is lost in the specimen drawn, thereby giving the erroneous suggestion of a difference between the position of the opening in *Relictus* and in other genera. The posterior flange (PF), which is directed obliquely outward from the ventral ramus, is rather weakly developed, leaving all of the opercular condyle (OC) exposed in lateral view. A line drawn from the apex of this condyle to the posteroventral tip of the ventral ramus does not intersect the posterior flange. The lateral ridge varies from moderately developed to nearly obsolete, as in the specimen illustrated. The area between the posterodorsal and opercular condyles

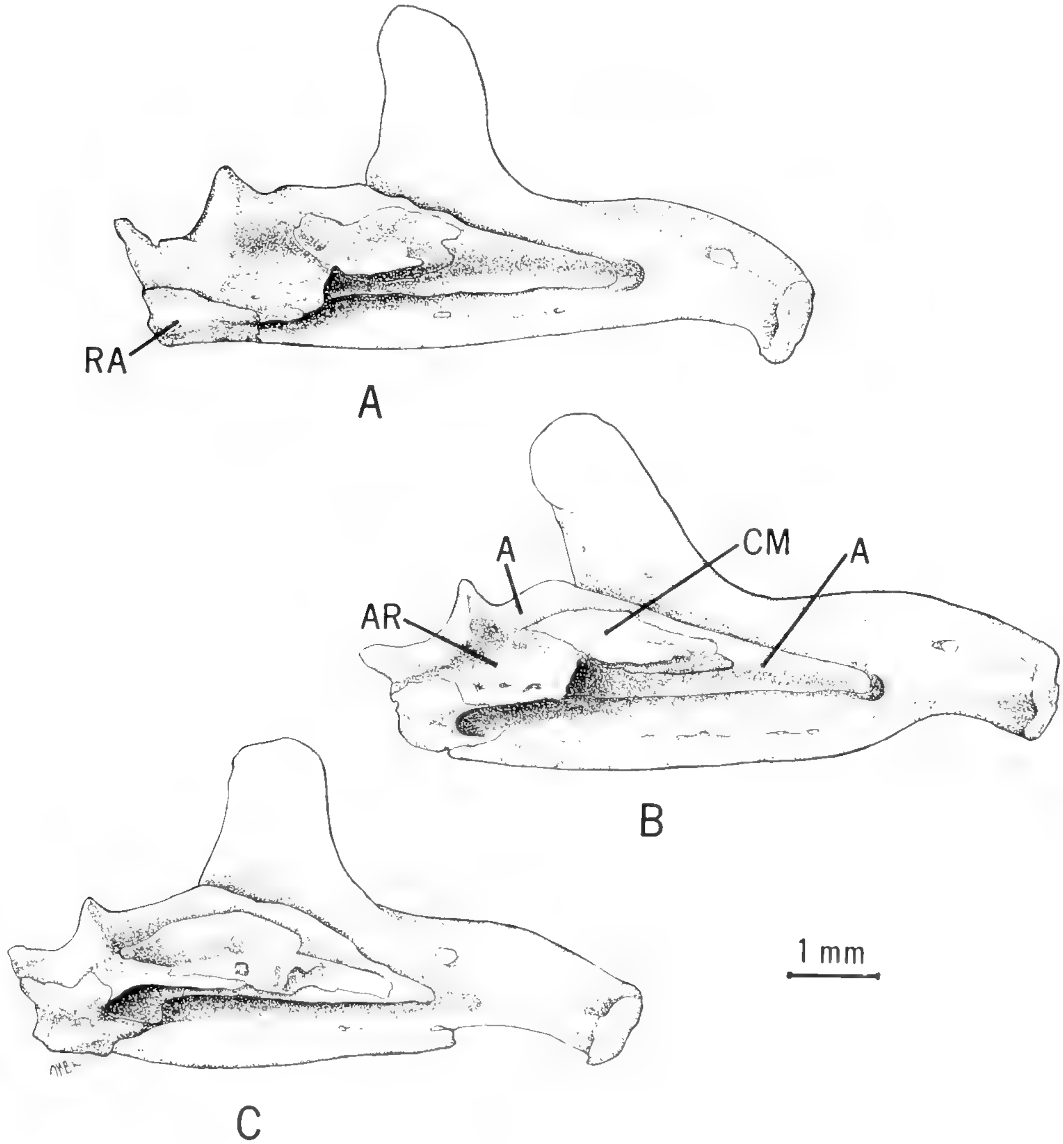


FIGURE 42. Mesial views of same lower jaws shown in figure 41. A, angular; AR, articular; CM, coronomeckelian (sesamoid articular); RA, retroarticular.

is long and broadly concave, as in the subgenus *Siphateles.*

On the mesial side of the hyomandibular, the position of the dorsal opening of the lateral hyomandibular foramen lies opposite or slightly below the level of the occipital condyle, well within the upper part of the bone, as in *Rhinichthys* (*osculus*), whereas in subgenus *Siphateles* (*Gila bicolor*) this foramen opens close to mid-length of the hyomandibular, well below the level of the occipital condyle.

The lower jaw is notably larger in *Relictus* than in any species of *Rhinichthys* (see figs. 41B,C, 42B,C), and the mandibular joint is less concealed by soft tissue (the mandible was not measured in *Rhinichthys* because the posterior end is less readily perceived than in most genera). The dentary, which forms the anterior and cen-

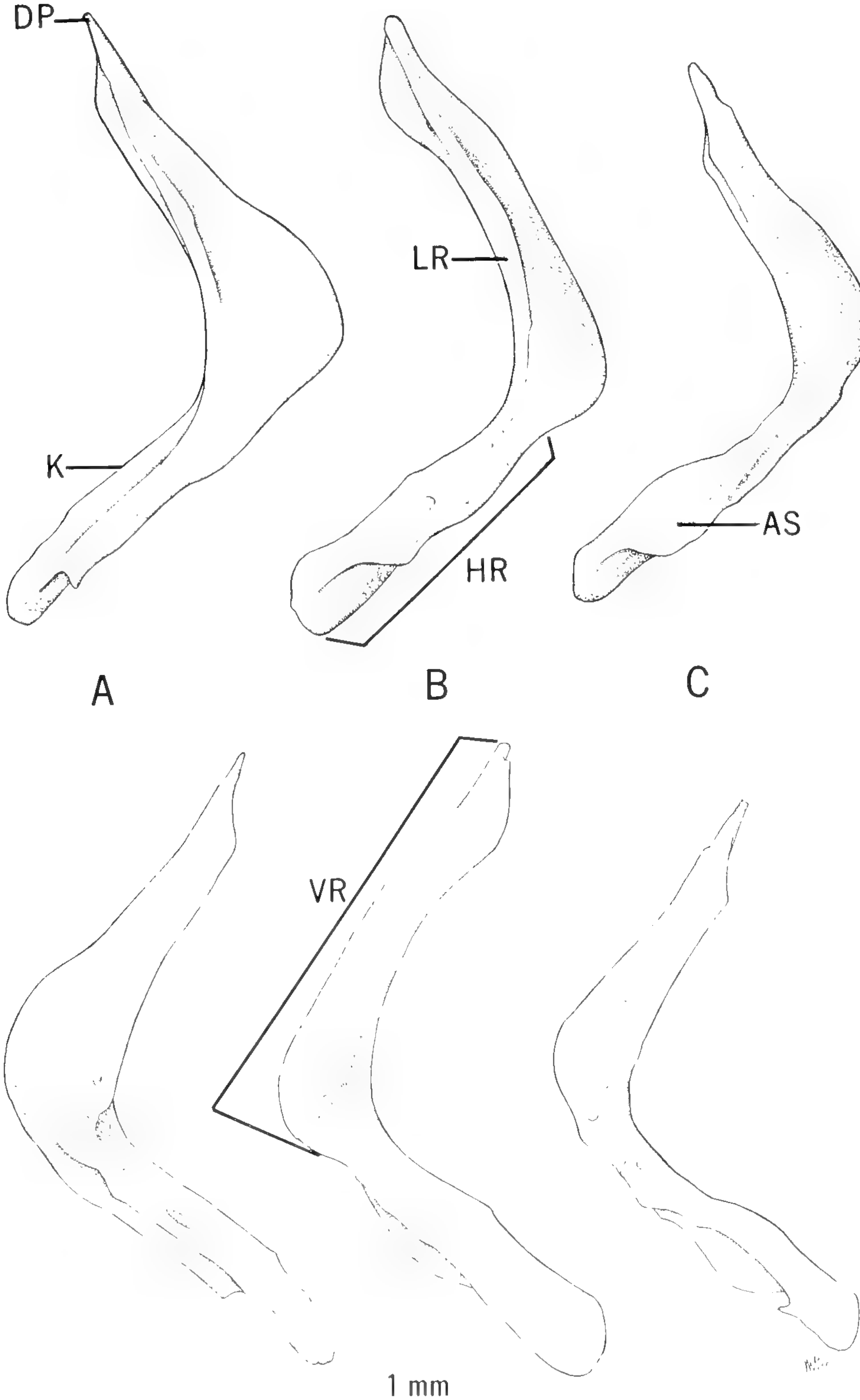


FIGURE 43. Lateral (above) and mesial (below) views of left cleithra of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (91 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ 124907). AS, anterior shelf; DP, dorsal process; HR, horizontal ramus, length; K, keel; LR, lateral ridge; VR, vertical ramus, length.

tral parts of each lower jaw, curves mesially at its anterior end to meet, at the midline, the anterior end of the opposite dentary. The bone bears a prominent ascending coronoid process (CP), which, in *Relictus*, lies well back on the dentary: the distance between the posterior end of the angular (A) and the rear margin of the process (at the level of the angular) enters more than three times in the length of the lower jaw. The coronoid process varies from narrow to broad and its anterior edge is slightly to strongly inclined posteriorly (as in *Gila copei*). Running along the ventrolateral surface of the dentary is the anterior part of the mandibular sensory canal. Lying laterally along the midside of the bone is the anterolateral foramen (AF); in *Relictus* this foramen lies well in advance of the tip of the angular, as it does also in *Gila* but not in *Rhinichthys* (figs. 41A–C).

The angular is long and pointed, as in *Gila*. Its posterodorsal surface is notched to receive the articulating surface of the head of the quadrate. Directly below the notch is a ventral excavation in which the retroarticular bone (RA) lies. The coronomeckelian bone (CM), or sesamoid articular, lies on the medial face of the angular near its midpoint and slightly below its dorsal margin.

The cleithrum (fig. 43B), a dermal bone, is the largest of the elements that comprise each pectoral girdle. In lateral view, the bone approaches the form of a reversed L, with the vertical ramus (VR) longer than the horizontal ramus (HR). The cleithrum bears a posterior winglike expansion, which is broadest near the posteroventral corner of the vertical ramus. A shelflike anterior expansion (AS) is developed from the horizontal ramus, which bears a keel (K, labelled "dorsal edge" by Uyeno and Miller, 1965, fig. 2) near the mesial edge. A narrow space mesial to this keel is partly sutured with the coracoid. Mesially, the anterior part of the cleithrum borders an oval interosseous space and contacts the coracoid at its tip. The lateral ridge (LR) of the cleithrum, which originates at or near the dorsal process (DP), is slightly deflected over the groove that lies along the anterodorsal part of the vertical ramus. Both the anterior shelf and the posterior expansion are relatively narrow in *Relictus*, and the anterodorsal flange is short and notably expanded. In general, the cleithrum of *Relictus* is rather slender, because the lateral shelf and anterodorsal flange are only moderately broadened.

The median urohyal (fig. 44B) is divided anteriorly into rather short left and right branches, each of which is usually further differentiated into dorsal and ventral divisions. A slender neck posterior to this bifurcation is immediately followed by three thin, backward-expanded wings, one vertical and two horizontal. The laterally expanded horizontal wings form the ventral surface, which is narrow-elongate, and concave along the midline. The depth of incision of the bifurcation varies from that drawn to at least twice as deep, and the width of the ventral surface may be a little greater than illustrated, but not nearly as broad as shown for *Gila bicolor* (fig. 44A). The urohyal is quite unlike that of *Rhinichthys* (fig. 44C).

Pharyngeal arch and teeth. We follow the nomenclature of Uyeno (1961, pp. 332–333, fig. 1). Each lower pharyngeal arch (fig. 45B) is strong and moderately heavy, about as in *Gila*, definitely more massive than in *Rhinichthys*. Neither limb is markedly flattened; the anterior limb (AL) is shorter than the posterior limb (PL). The anterior angle (AA) on the convex edge is usually sharply produced and the surface toward the angle is notably flat, with a very thin edge. The characteristically deeply pitted surface (P), through which blood vessels and nerves pass, is so very thin that in some individuals either one or both arches may be perforated by a small to large foramen, or by several foramina. The rather swollen convex face near the base of the teeth lacks any trace of an alveolus and does not provide a flat enough shelf on which a tooth could develop. A posterior angle (PA) also tends to be developed. The anterior edentulous process is shorter than the posterior edentulous process, or

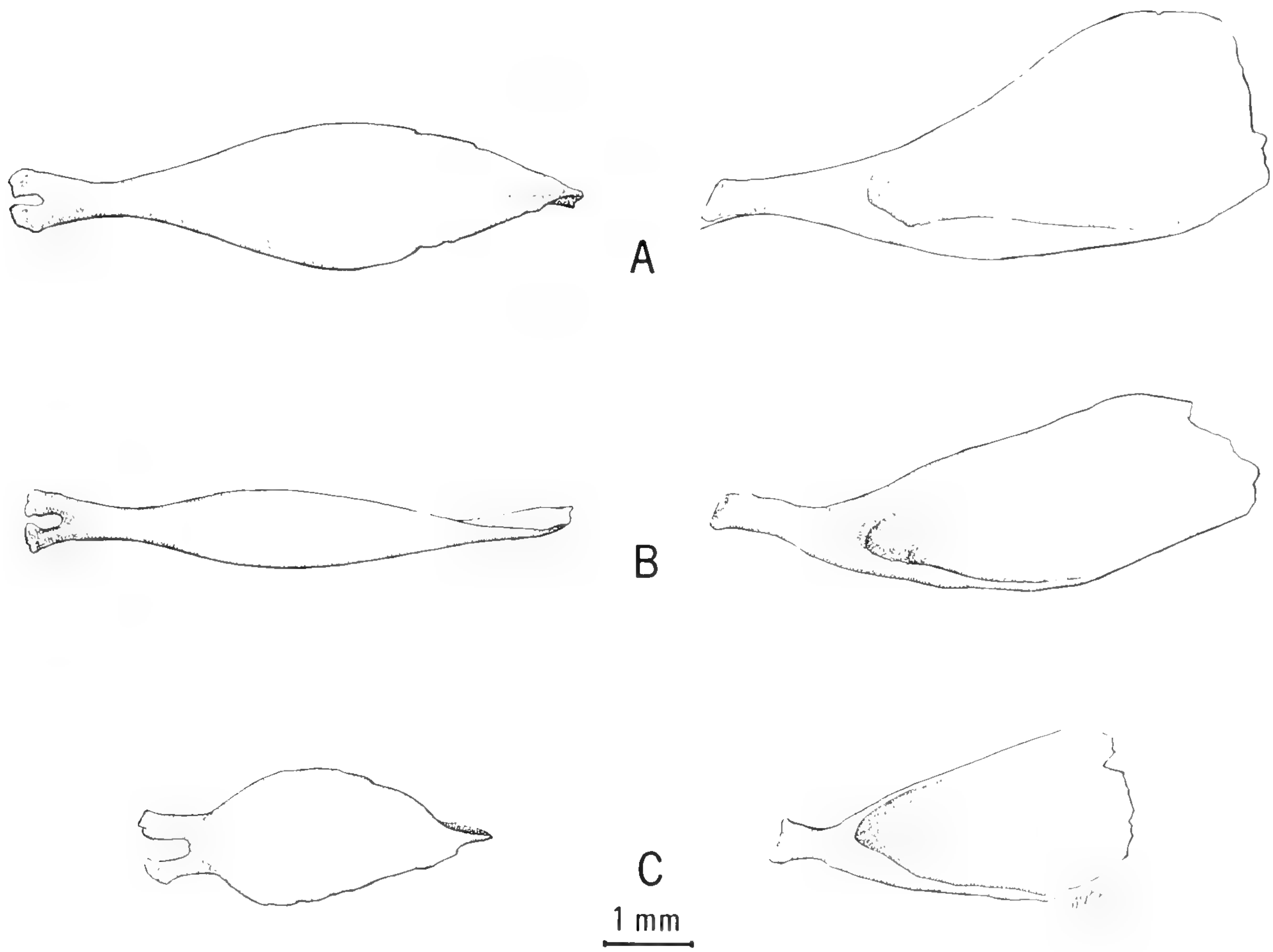


FIGURE 44. Ventral and lateral views of the urohyals of adult females of: A, *Gila bicolor isolata* (paratype, 79 mm., UMMZ 186518); B, *Relictus solitarius* (81 mm., UMMZ 177095); C, *Rhinichthys osculus* subspecies (75 mm., UMMZ 173790, from Little Bear River, Utah).

equally long. Tooth I rises relatively close to the front edge of the posterior limb. The dentigerous part of the arch differs sharply from that of subgenus *Siphateles* in not being markedly elevated posteriorly.

The pharyngeal teeth are all heavy and are moderately to very weakly hooked, or the anteriormost one (IV, represented by its alveolus in specimen figured) may lack a hook in large individuals. There is a definite grinding surface on most of the teeth. The tooth formula (table 33) is normally 4—4, with occasional noteworthy variation (p. 93) to 4—3 and 5—4 (with the higher number, as usual, on the left side). When

TABLE 33. *Dental formulas in certain Collections of* Relictus solitarius *from different drainage basins.*

Pluvial lake system (Coll. no.) Valley	Formula[1]		
	0,4—3,0	0,4—4,0	0,5—4,0
Lake Franklin			
Ruby (1–3, 5, 6)	—	9	—
Butte (10, 11)	1	11	—
Lake Gale (13)	—	5	—
Lake Waring (16, 17, 19)	1	14	1
Lake Steptoe (22, 25, 27, 28)	—	15	1
Lake Spring (33, 34)	—	17	—
TOTAL	2	71	2

[1] Counted left-right; alveoli included.

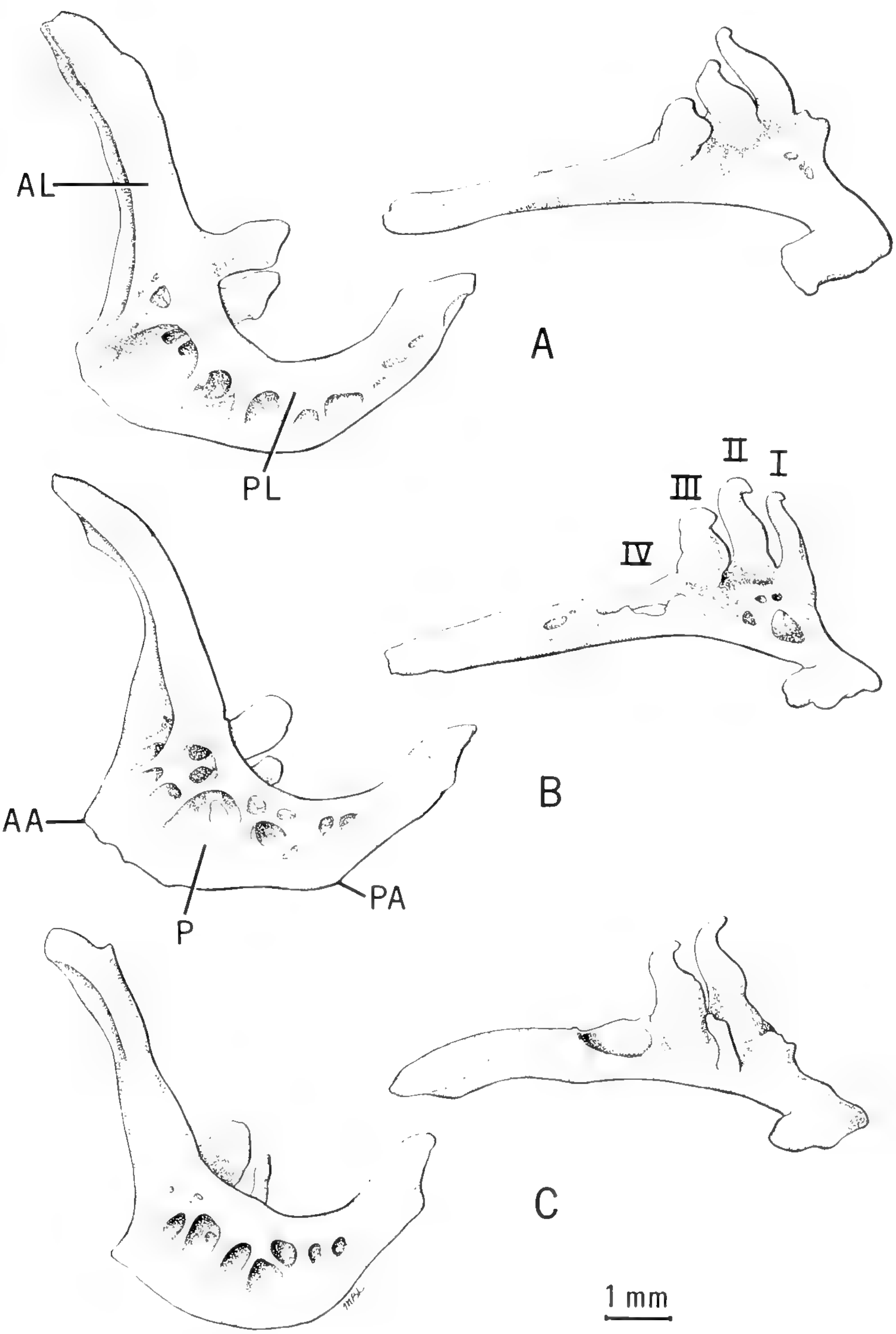
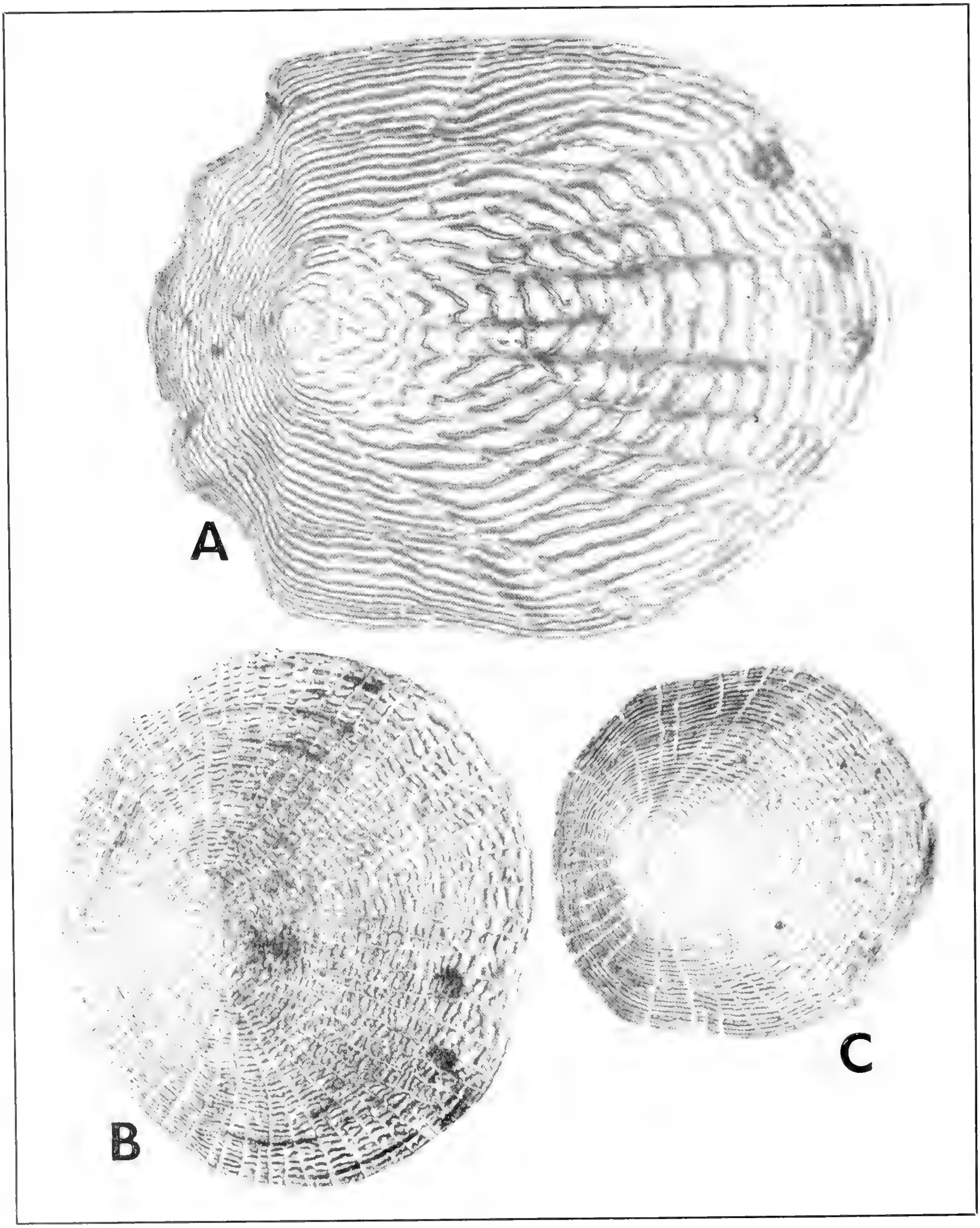


FIGURE 45. Dorsolateral (left) and mesial (right) views of pharyngeal arches and teeth (or alveoli) of adult females of: A, *Gila bicolor isolata* (paratype, 88 mm., UMMZ 186518); B, *Relictus solitarius* (91 mm., UMMZ 177095); C, *Rhinichthys osculus reliquus* (paratype, 85 mm., UMMZ 124907). AA, anterior angle; AL, anterior limb; P, pitted surface; PA, posterior angle; PL, posterior limb; I–IV, teeth of major row in the arch of *Relictus* (IV represented by alveolus); in the arch of *Gila*, the first tooth, and in the arch of *Rhinichthys*, the first and fourth teeth of the major row, are represented by alveoli.


A
B
C

only three teeth are developed, the arch ascends abruptly to the base of both tooth I and tooth III, leaving no flattened space for another tooth, and showing no sign of an injury.

Scale structure. The scales (fig. 46B), typically, are vertically oval, with the focus far removed from the posterior edge (nearer the front edge). The circuli are rather regular and persist along the anterior field, in which, due to the small size of this field, they are notably crowded. Radii are numerous on all fields. The development of basal radii is correlated, as usual, with the rather deep embedding of the scales. Among western cyprinids, radii are developed on all fields of the scales in all species of *Rhinichthys* (though weak or obsolete on the basal field in the very distinctive *R. falcatus*) and in the monotypic genera (as currently recognized) *Acrocheilus, Agosia, Eremichthys, Moapa, Orthodon*, and *Tiaroga*; also in some species of *Gila* (in both subgenera, *Gila* and *Siphateles*) and, to a varying degree, in some forms of *Hesperoleucus*.

Pseudobranchiae. The pseudobranchiae though rather long are usually more or less completely bound down to the opercular tissues. This same arrangement we find in *Gila bicolor* and *Rhinichthys osculus*, and also in *Moapa coriacea* and *Eremichthys acros*, contrary to our statements (1948a, pp. 2, 15) that the relict genera *Moapa* and *Eremichthys* lack pseudobranchiae.

Relationships

Relictus, as indicated previously, has several distinctive osteological traits, of which at least one (the narrow supraethmoid; fig. 39) is most similar to that of *Rhinichthys* (table 34). The dental formula could have been derived from that of *Rhinichthys* or, just as plausibly, from *Gila*. The lack of a frenum and a barbel, and the presence of radii on all fields of the scale, have limited value in determining relationships because these structures may be lost or independently derived among surviving populations of several genera of western cyprinids. The moderate vertebral number may simply represent the retention of a generalized condition. The pigmentation (described on pp. 209–212), bears a striking resemblance to that of the subgenus *Siphateles*, although the simple intestine again is more like that of *Rhinichthys*. The distinctive karyotype (see below) is most closely approached, among western minnows thus far karyotyped, by that of *Gila (Siphateles) bicolor*.

From these observations and from geographical and paleohydrographic considerations, we consider it probable that *Relictus* is an old relict (likely pre-Pliocene) that was derived from an ancestral line from which the groups we refer to *Gila* and *Rhinichthys* were both also derived. Among living species of *Gila*, the generalized Utah chub (*Gila atraria*), despite its consistently biserial dentition, is probably a near relative, along with *Gila (Siphateles) bicolor*. However, the combination of primitive and derived traits render the precise relationships of *Relictus* difficult to evaluate.

Karyotype. Among the monotypic and polytypic western genera of cyprinid fishes that logically may represent the closest relatives of *Relictus* (table 34), the chromosome number and morphology (figs. 47, 48) of the new genus stand distinctly apart (Uyeno and Miller, in preparation).

The karyotype is distinguished by a relatively large number of acrocentric chromosomes (2 large and 8 small) but also many that are metacentric (12). The remaining 28 chromosomes are subtelocentric and submetacentric, yielding a diploid number of 50, characteristic for all American cyprinids thus far examined (about 60 species have been determined by Teruya Uyeno).

←

Figure 46. Typical scales of adult females of three species of Cyprinidae from Nevada. A. *Gila bicolor obesa* (considered topotypic): 90 mm.; Humboldt River near Lovelock (G2); UMMZ 124873. B. *Relictus solitarius* (paratype): 90 mm.; Kirkpatrick Ranch, Butte Valley (Collection 7); UMMZ 141518. C. *Rhinichthys osculus robustus*: 73 mm.; Indian Creek, tributary to Reese River; UMMZ 124894. Photographed by Louis P. Martonyi.

TABLE 34. *Comparisons between* Relictus *and certain other western genera of Cyprinidae.*[1]

Character	*Rhinichthys*	*Relictus*	*Gila*	*Eremichthys*	*Moapa*	*Agosia*
Supraethmoid (fig. 39)	Long, narrow	Like *Rhinichthys*	Short, broad	Like *Gila*	Like *Gila*	Like *Gila*
Dentition (normal)	1,4—4,1 or 2,4—4,2	0,4—4,0	Variable, 1 or 2 rows	0,5—4,0	0,5—4,0	0,4—4,0
Barbel	Present[2]	None	None	None	None	Present
Frenum	Present or not[3]	None	None	None	None[4]	None[4]
Scales in lateral line	35–90	50–70	40–90	70–80	70–80	70–90
Scale radii (fig. 46)	On all fields[5]	On all fields	Basal radii usually lacking	On all fields	On all fields	On all fields
Anal rays	Typically 7	Typically 7	6–11	7 or 8	7 or 8	7
Gill-rakers	5–10, usually 6–8	7–12	5–40	9–11	5–9	About 6–8
Vertebrae	35–41	35–39, usually 36 or 37	38–49	34–36	36–38	36–39
Preoperculomandibular pores	8–13	11–19	13–30	9–12	10–14	8–11
Supratemporal canal	Complete or incomplete	Incomplete	Complete or incomplete	Usually complete (27 of 30)	Complete (29 of 30)	Complete or incomplete
Origin of dorsal fin	Behind pelvic insertion (except in *R. falcatus*)	Slightly before to slightly behind pelvics	Over or behind pelvics	Behind pelvics	Over or slightly behind pelvics	Over or slightly behind pelvics
Development of lateral line	Variable	Incomplete; rarely as far as D. origin	Complete (rarely disrupted)	Variable; incomplete in ca. 25%	Complete (rarely disrupted)	Complete
Peritoneum	Variable; dark brown or silvery (with puncticulations)	Silvery, with brown puncticulations	Variable	Brownish, with admixture of black pigment	Blackish	Blackish brown
Intestine	Single loop	Like *Rhinichthys*	Single loop with bend	Much coiled	Single loop with bend	Slightly coiled
Type ("Group" of Kafuku, 1958)	1	1	2 (with variations)	4 (modified)	2	4 (basic)

[1] See also generic description, especially for other osteological characters, and note on karyotype
[2] Barbel lacking on one or both sides in some populations, particularly in isolated waters.
[3] Frenum developed in subgenus *Rhinichthys*; lacking in subgenus *Apocope*, except variably developed in Colorado River system; lacking in *R. falcatus*.
[4] Hidden frenum present.
[5] Anterior radii weak or obsolete basally in *R. falcatus* (perhaps generically separable).

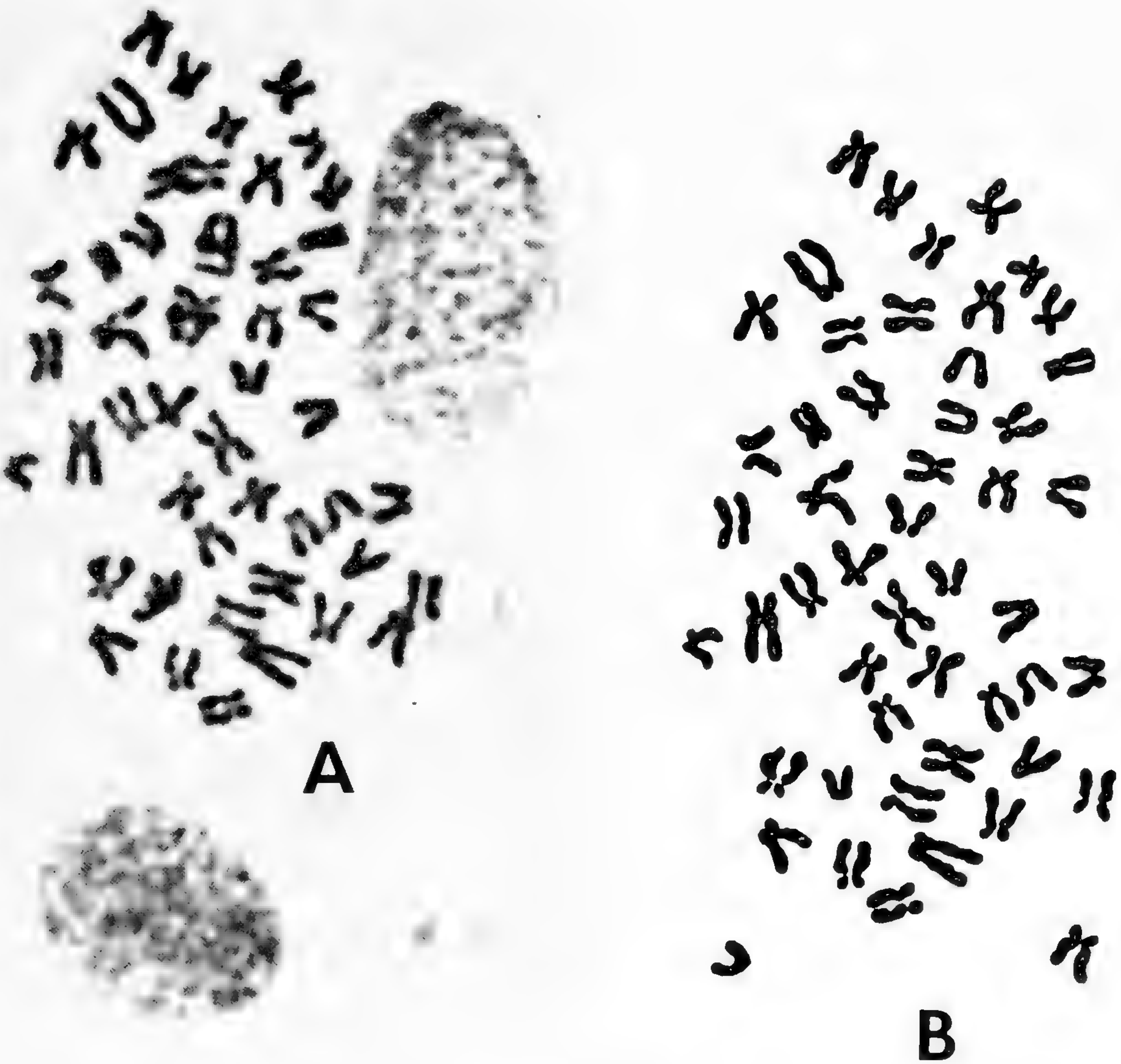


FIGURE 47. Karyotype of *Relictus solitarius*, processed by Teruya Uyeno in 1971. A, photograph of squash preparation. B, tracing of chromosomes, with some displacement where overlapping. The chromosome categories are analyzed and grouped in figure 48.

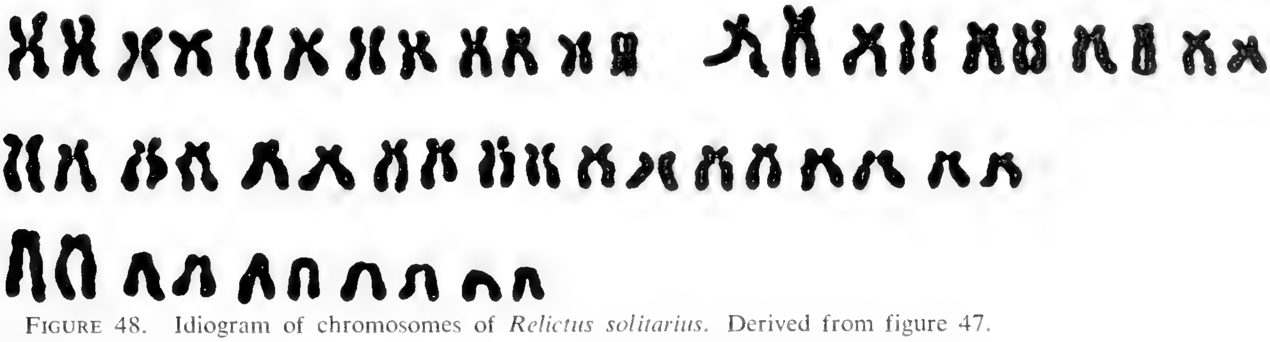


FIGURE 48. Idiogram of chromosomes of *Relictus solitarius*. Derived from figure 47.

In the idiogram (fig. 48), the 12 chromosomes interpreted as metacentric are set apart in the first row, followed in the next two rows by the 28 that are more or less transitional between metacentric and acrocentric, then, in the last row, by the 10, 2 large and 8 small, that are classed as acrocentric. Among the western genera mentioned above, the karyotype of *Relictus* is perhaps most closely approached by that of *Gila (Siphateles) bicolor*, which also has 2 large but 6 small acrocentric chromosomes and 16 metacentric ones. *Gila (Gila) robusta* has only 2 large and 4 small acrocentric chromosomes and 12 metacentric ones. *Rhinichthys* resembles *Relictus* in having 6 or 8 acrocentric but only 6 metacentric chromosomes (Uyeno and Miller, in preparation).

Derivation of name. The Latin *relictus* is the past participle of *reliquo*, to leave behind, and is also a noun, meaning a forsaking or abandoning. It is interpreted as a substantive, as in the English 'relict,' in the sense of the relict one. The gender is masculine.

Relict Dace

Relictus solitarius Hubbs and Miller.
(Figures 35C,D, 51.)

Relictus solitarius Hubbs and Miller, 1972, p. 102 (diagnosis).

Holotype, UMMZ 186904, a nuptial male 60.3 mm. in standard length (fig. 35C). Paratypes, all other specimens (170, 34–99 mm. long) from same Collection (no. 7: data given below), including the mature female, 89.8 mm. long, that is illustrated (fig. 35D). All other specimens studied are listed below with an account of the status of the populations, but no others are designated as types.

The discovery of this unique relict species is recounted under the heading of the genus. It occurs only in the contiguous drainage basins of the following pluvial lakes just south of the conjoining parts of the Lahontan and Bonneville basins, in eastern Nevada: *Lake Franklin* and its tributary *Lake Gale*, in Ruby and Butte valleys, respectively, where native; *Lake Waring* and the tributary *Lake Steptoe*, in Goshute and Steptoe valleys, respectively, where also native; and *Lake Spring*, in Spring Valley, where almost surely introduced. The paleohydrography and the remnant waters of these ancient lakes are treated above (pp. 38–58). The evidence now seems conclusive that *Relictus solitarius* is the only native fish in the expanse of 14,682 square kilometers that drained indirectly and directly into Lake Franklin and Lake Waring. It is probable that the species originally was relict in only one of the two main drainage complexes, but gained access to the other by stream wandering over a bajada across the low intervening Goshute Pass (p. 43).

Within the entire north-central part of the Great Basin herein under treatment, this is by far the most numerous of the four native fish species, and it occupies about as many of the isolated spring waters as harbor the other three. It occurs in isolated springs and in springfed streamlets.

The at least temporary establishment of this species in Spring Valley, to which we now assume it was not native, we attribute (p. 235) to its introduction from one of the north-central Great Basin valleys in which it is native. There is some indication, furthermore, that it was once stocked in a spring in Utah (p. 226).

Material Examined and Population Status.

Our Collections (table 35), with some supplementation (p. 205), have provided a vast abundance of preserved material: 7,501 specimens in 34 Collections, of which only 7 essentially duplicated a prior Collection. These Collections appear to represent the entire range of the species. In 1971 a few additional specimens from previously sampled springs were taken, for identification and for their bearing on survival.

We list the data in some detail, for the bearing they have on the ecology of this relict fish and on the population changes that have occurred, or

TABLE 35. *Data on collections of* Relictus solitarius.

Coll. No.	Location	Field No.	Museum	Cat. No.	No. specimens	Size, mm.	Map: fig.
	Lake Franklin drainage						
	Ruby Valley						
1	Borrow pit	Lewis 4	UMMZ	186898	70	18–30	8
2	Pothole spring	M 34-209	UMMZ	132188	317	14–59	8
3	Isolated spring	Lewis 5	UMMZ	186899	43	17–50	8
4	Slough below Cave Cr.	M 34-210	UMMZ	132189	18	24–39	8
5	Isolated spring	Lewis 3	UMMZ	186901	10	10–17	8
6	Isolated spring	Lewis 1	UMMZ	186900	5	24–27	8
	Butte Valley						
7	Kirkpatrick Ranch	H 42-47	UMMZ	141518 186904[1]	170 1	34–99 60	8, 12
8	Atwood Ranch (= 7)	M 34-212	UMMZ	132191	277	21–99	8, 12
9	Atwood Ranch	JED 64-53	UNLV		35	21–84	8, 12
10	Trib. Butte Cr.	M 34-211	UMMZ	132190	225	14–98	8, 12
11	Head, Odgers Cr.	H 42-46	UMMZ	141517	205	24–77	8, 12, 14
	Lake Gale drainage						
	Butte Valley						
12	Stratton Ranch	JED 64-52	UNLV		67	19–81	8, 12, 14
13	Wrights Spring	H 42-45	UMMZ	141516	97	27–64	8, 12, 14
14	Stratton Ranch	H 42-44	UMMZ	141515	383	11–72	8, 12, 14
15	Owens Ranch	H 42-43	UMMZ	141513	219	25–72	8, 12, 14
	Lake Waring drainage						
	Goshute Valley						
16	Johnson Ranch (meadow)	H 42-42	UMMZ	141511-12	171	7–99	12
17	Johnson Ranch (slope)	H 42-41	UMMZ	141509-10	706	16–114	12
18	Phalan Creek	M 38-165	UMMZ	124966	168	26–93	8, 12
19	S. of Currie	M 38-164	UMMZ	124963	201	23–87	8, 12, 14
	Lake Steptoe drainage						
20	Cardano Ranch	M 38-162	UMMZ	124962	257	17–93	8, 12, 14
21	Warm Springs Station	JED 62-27, pt.	UNLV	F 175	147	12–42	8, 14
22	Campbell Ranch	M 38-166	UMMZ	124967-68	341	15–87	8, 14
23	Steptoe Ranch (= 22)	JED 62-27, pt.	UNLV	F 174	150	13–41	8, 14
24	Grass Springs	JED 62-27, pt.	UNLV	F 169	155	21–63	8, 14
25	Dairy Ranch	M 38-160	UMMZ	124956-57	367	13–81	8, 14
26	Georgetown Ranch	M 38-158	UMMZ	124954	403	15–81	8, 14
27	Ruth Pond	—		—	6	—	8, 14
28	3C Ranch	M 38-159	UMMZ	124955	209	17–89	14
29	Fish Pond Springs (= 28)	M 69-15	UMMZ	188959	289	20–82	14
	Lake Spring (introduced)						
30	Springs, Spring Valley Cr.	JED 64-43	UNLV		80	27–67	12, 14
31	Springs, Spring Valley Cr.	JED 64-56	UNLV		99	16–66	12, 14
32	Stone House	M 38-48	UMMZ	124786	1,073	14–88	12, 14
33	Stone House	M 59-90	UMMZ	177095	498	14–81	12, 14
34	Keegan Ranch	M 59-89	UMMZ	177094	39	10–22	14

[1] Holotype.

may be anticipated, as a result of human activities. Locations of springs are specified so as to permit relocation for future checking. Evidence that we have gathered concerning the population status of the species is presented in this section.

The Collections are serially listed under valleys (all in Nevada), from west to east, and within each valley from north to south. For this species we list Collections separately, even when they duplicated a previous sampling.

POPULATIONS OF RUBY VALLEY IN FORMER DRAINAGE BASIN OF PLUVIAL LAKE FRANKLIN. From Ruby Valley, which in pluvial times was largely occupied by the main body of Lake Franklin (pp. 39–45), we have examined 463 speci-

mens from six Collections (1–6), which seemingly represent most of the Recent range in the valley of this species—and of all native fish life in the basin, unless, as seems highly improbable, trout and/or chubs (*Gila bicolor*) were native in the mountain streams and in Ruby Lake, respectively.

It is virtually certain that the relict dace was native in Ruby Valley, for King (1878, p. 504, here quoted on p. 44) mentioned the occurrence of fish, presumably of this species, in Ruby Lake. On September 12–13, 1934, when he first explored the basin, Hubbs found the dace abundant in the springs and sloughs of Ruby Lake, which occupied much of what had been the southern arm of pluvial Lake Franklin. Close to Collection 2, from a single spring, the dace was found to be common on the gently sloping grassy bed of pluvial Lake Franklin in other waters examined: (1) in other pothole springs, including one about 2 m. in diameter and covered with 'blanket moss' (in these other springs numerous young about 15–30 mm. long indicated late spawning); (2) in the rather swift, *Nasturtium*-containing outlet of a large stony seepage spring; and (3) in a large slough about 25 cm. deep within a large rushy marsh, which, with the sloughs along its western edge, constituted the bed of Ruby Lake (this marsh contained many ducks, which would have been hunted later in the fall). Fish were lacking in icy-cold Cave Creek (both within and below the cave) and in several large cold springs arising nearby from the same limestone formation. The fish was well known to residents as the "tule minnow" (a vernacular that was appropriate locally, but definitely is not applicable throughout most of the range of the species).

A long-time rancher, W. J. Gardner, whose home ranch was on Gardner Creek, a tributary to the present Franklin Lake, reported to us in 1934 that on the east side of Ruby Lake he knew of minnows occurring only, and intermittently, in a small spring three-fourths of a mile from Minnie Spring, which is southwest of the hot springs near the north end of the lake, but that Minnie Spring (presumably not named for minnows) was fishless (however, they were reported to be there later, by Donald E. Lewis). In 1932 Gardner had found "minnows" in a slough near his home ranch, after Franklin Lake, usually dry, had water; he thought these had come out of a tributary canyon, but that they did not seem to be young trout.

During our 1942 trip two ranchers in northeastern Nevada testified regarding fish in Franklin River, the main stream course in the northern part of Ruby Valley leading toward Franklin Lake. One told of seeing small fish in the stream about 1937, but another thought it to be fishless, because of its tendency to dry up (we had found it dry in 1934). On June 28, 1942, Hubbs examined the then flowing stream closely for about one-fourth mile on either side of the Ruby Lake Road, without locating a fish.

Clearly, as late as 1934, the relict dace abounded in the profuse spring-fed waters of the Ruby Lake complex, but it is not certain that it occurred elsewhere in Ruby Valley.

In 1965, Hubbs found that the dace had seemingly been extirpated in at least much of Ruby Valley, presumably as a result of the extensive development of a sport fishery, principally for largemouth bass (*Micropterus salmoides*), promoted by popular posters and leaflets and serviced by two special landings with ramps for boats. The Nevada Fish and Game Department was operating a fish hatchery within the limits of the Ruby Lake National Wildlife Refuge (which also manages a public shooting area within the Refuge). The late J. Clark Salyer, head of the federal wildlife refuges, established the policy of protecting the endemic minnow by such means as prohibiting importation of bait minnows, but under the management practices of 1965 the minnow seemed doomed in Ruby Valley. In fact, not a single minnow was seen in that year during an examination of ten clear-water springs of various types in the long file emerging along the west edge of the basin, very close to the boundary between the Ruby Mountains bajada and the

marshland representing the floor of Ruby Lake, from just south of Shanty Town for more than 4.8 km. to one of the Ramirez Springs (all in T. 26 N., R. 57 E.).

However, at our request, Donald E. Lewis, Manager of the Ruby Lake National Wildlife Refuge, had his staff search for minnows throughout the refuge on August 2–14, 1967. This search led to the collection of *Relictus* at four places, as is detailed in the following list. Mr. Lewis reported:

> The small fish are most abundant in isolated water where the largemouth bass cannot reach them. However, I believe the fish does exist throughout the lake, but is greatly reduced by largemouth predation. All fish samples except No. 4 [Collection 1] were taken from isolated springs. No. 4 is an isolated dike borrowpit without a bass population.

Mr. Lewis had earlier reported (personal communication, November 12, 1965) having seen minnows about Ruby Lake at the North Sump (in NW ¼ Sec. 5, T. 27 N., R. 58 E.) on the west side of the lake; along the CCC Dike running across the lake near the northern edge of Sec. 22, in same township; at Minnie Spring, near center of Sec. 10, in same township (where earlier reported absent); and at one place, where some were later sampled (Collection 5). He indicated that minnows do not occur in the Hot Springs (Sec. 2, T. 27 N., R. 58 E.), about 1 mile northeast of Minnie Spring.

Collection 1 (fig. 8). Isolated borrow pit on border of flat of Ruby Lake, 0.8 km. east of western border of Wildlife Refuge, north of middle of Sec. 14, T. 27 N., R. 58 E.; Elko County, ca. 12 km. north of White Pine County. Donald E. Lewis, August 10, 1967 (Sample no. 4); UMMZ 186898 (70, 18–30 mm.).

Collection 2 (fig. 8). Pothole spring on gentle grassy slope on old lake bed, on western side of Ruby Lake, ca. 10 km. south of Harrison Pass, at elevation of ca. 6,000 feet (1,829 m.); in or near Sec. 19, T. 27 N., R. 58 E.; Elko County. Moderately clear water (bottom visibility ca. 1.5 m.); soft mud, with some stones and slabs; slight outflow; much *Chara*, *Nasturtium*, and rushes—generally thick—but open in deep holes; cold. Hubbs family, September 12, 1934 (M34–209); UMMZ 132188 (317, 14–58 mm.); 6-foot woven-mesh seine and 15-foot seine with ¼-inch square mesh.

Collection 3 (fig. 8). Isolated spring between county road and the Ruby Lake flat 0.7 km. east of western boundary of Wildlife Refuge, Sec. line 18–19, T. 27 N., R. 58 E.; Elko County, 10.5 km. north of White Pine County. Lewis, August 14, 1967 (Sample no. 5); UMMZ 186899 (43, 17–50 mm.).

Collection 4 (fig. 8). Slough below Cave Creek on west side of Ruby Lake, in T. 27 N. near western border, about middle of R. 58 E.; Elko County. Moderately clear water; very soft bottom (collector sank 0.3–0.6 m. into the mixture of clay and sand); no apparent current; little vegetation (rushes and grass); moderate temperature. Hubbs family, September 13, 1934 (M34–210); UMMZ 132189 (18, 24–39 mm.); 6-foot woven-mesh seine.

Collection 5 (fig. 8). Isolated spring near western border of Wildlife Refuge, just above lake flat, 0.3 km. south of northern border of T. 26 N., at R. 57–58 E. border; Elko County, 4.5 km. north of White Pine County. Lewis, August 9, 1967 (Sample no. 3); UMMZ 186901 (10, 10–17 mm.).

Collection 6 (fig. 8). Isolated spring 0.4 km. south of southern boundary of Wildlife Refuge, in NE ¼ Sec. 12, T. 25 N., R. 57 E.; White Pine County, 7 km. south of Elko County. Lewis, August 2, 1967 (Sample no. 1); UMMZ 186900 (5, 24–27 mm.).

In addition, Mr. Lewis provided one sample (R3) of a presumably introduced minnow, *Rhinichthys osculus robustus* (pp. 107–109).

Populations of that part of Butte Valley formerly directly tributary to Pluvial Lake Franklin. Five Collections (7–11), comprising 913 specimens, adequately represent *Relictus solitarius* in the northern part of Butte Valley, Nevada, that in pluvial time drained directly into Butte Bay of Lake Franklin. Included is the type series of the species. Southward this area grades into the similarly spring-rich, fish-inhabited northern part of the section of Butte Valley that drained into pluvial Lake Gale. The whole valley to the north and west of Kirkpatrick (Atwood, Don Phalan) Ranch (Collections 7–9) appears from our field reconnaissance, from maps, and from local testimony, to be devoid of adequate habitat and of fish life. The informants included Jerome Phalan Stratton, White Pine

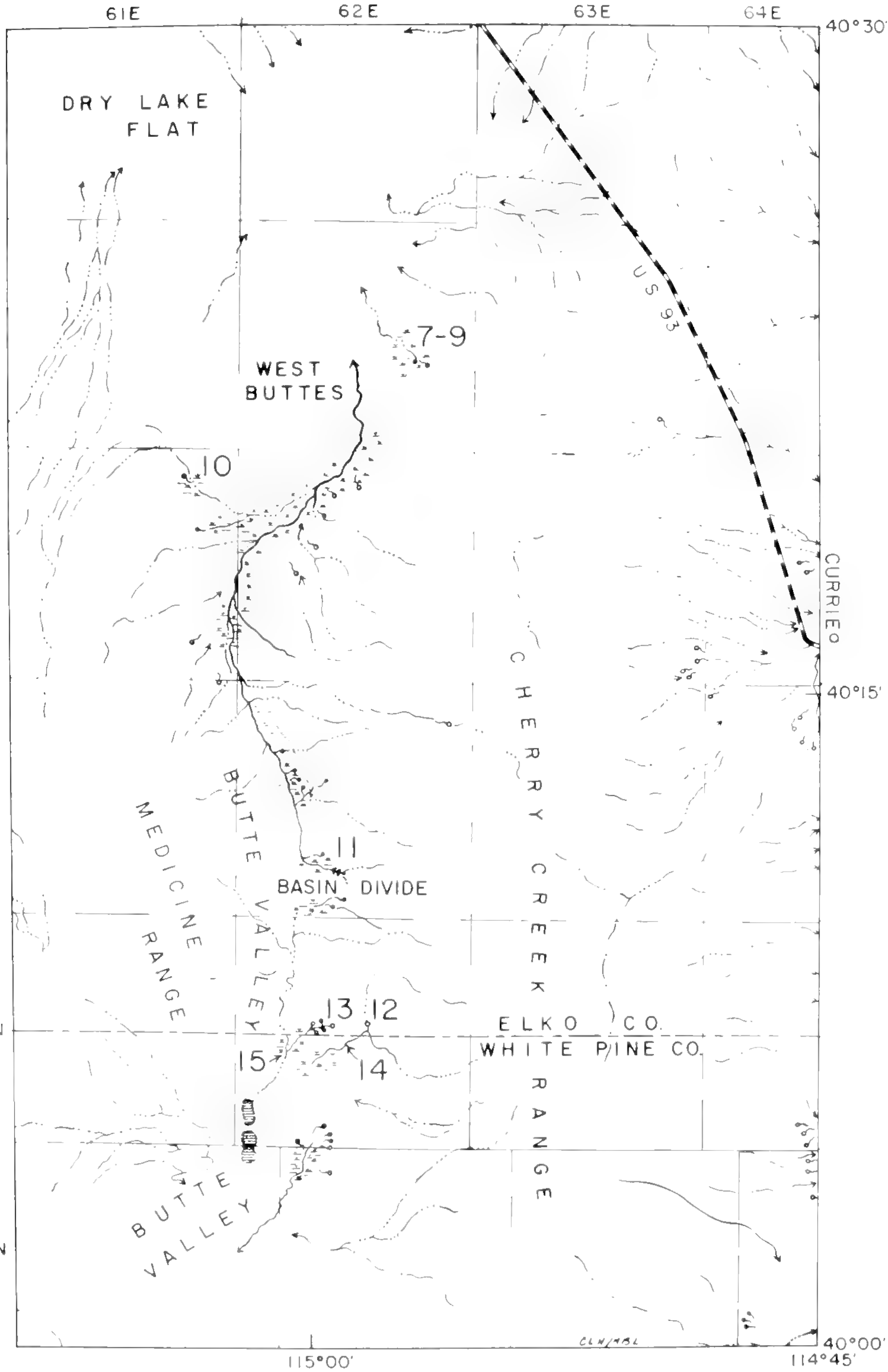


FIGURE 49. Springs, spring creeks and meadows, intermittent streams and washes, and county and township lines, in the spring-bearing, northern part of Butte Valley, and adjacent regions, in Elko and White Pine counties, Nevada. Based on U.S. Geological Survey National Topographic Map, 1:250,000 series, Elko Sheet (1958), and Map of White Pine County, by Ed. Millard & Son, Ely, Nevada (1930); and on field reconnaissance by authors. Numerals refer to Collections of *Relictus solitarius* (see pp. 197–202).

County Road Supervisor and owner of Stratton Ranch.

The hydrography of both drainages of Butte Valley (fig. 49) has been described by Glancy (1968).

Collection 7 (figs. 8, 12, 49). Ditch from upper, hillside spring on Kirkpatrick Ranch (in 1934 called "Atwood Ranch," later called "Don Phalan Ranch"), lowest and northernmost spring water in valley, on east side north of the narrows, where opening onto lake flat in east part of T. 29 N., R. 62 E. (same location as for next two entries); Elko County, ca. 21 km. northwest of Currie. Clear water of fine taste; rather firm clay; rather slow current; little *Potamogeton*, cf. *P. pectinatus*; 18° C. (air 21°). Hubbs family, June 27, 1942 (H42–47); UMMZ 186904 (holotype, 60.3 mm.) and UMMZ 141518 (170 paratypes, 34–99 mm.); one haul of a 6-foot woven-mesh seine.

Collection 8 (figs. 8, 12, 49). Springs on flat area of Atwood Ranch (later "Kirkpatrick," then "Don Phalan" Ranch; same location as for Collection 7). Clear water; very soft false bottom at depth of ca. 2.0 m.; moderate outflow; nearly choked with *Chara*, *Utricularia*, *Myriophyllum*, etc.; moderate temperature. Hubbs family, September 13, 1934 (M34–212); UMMZ 132191 (277, 21–99 mm.); 25-foot seine with ¼-inch square mesh in bag.

Collection 9 (figs. 8, 12, 49). Spring on same ranch as for Collections 7 and 8. Clear water; gravel and mud; depth to ca. 1 m.; dense vegetation; abundant aquatic invertebrates; 18° C. (air 21°); J. E. Deacon and M. B. Rheuben, September 14, 1964 (JED 64–53); UNLV (35, 21–84 mm.); 15-foot seine with ¼-inch square mesh. The spring source had been dredged out (banks as high as ca. 3 m.).

Collection 10 (figs. 8, 12, 49). Western tributary of Butte Creek, fed by springs on property of Silver Butte Mining Co. (formerly "Quilici Ranch," but known as "Delker Spring" in 1942); north of narrows of valley, in northeast part of T. 28 N., R. 61 E.; Elko County. Clear water; moderately soft mud; moderate current; choked with *Nasturtium*, algae, etc.; moderate temperature (warmer in summer). Hubbs family, September 13, 1934 (M34–211); UMMZ 132190 (225, 14–98 mm.); 6-foot woven-mesh seine.

Collection 10 was made in the first spring north (ca. 2.4 km.) of Taylor Ranch (then a division of Odgers Ranch), on which the colder spring and its swift outlet, which was about 1.5 m. wide and irrigated a large meadow, seemed to be fishless (residents thought that clearing, damming, and flushing of this spring creek may have killed minnows formerly present). This spring is probably the one ("28/61–11d1") mapped and treated by Glancy (1968) and shown on the cover illustration of his report. According to testimony of a former resident, springs at Odgers Home Ranch, ca. 8 km. south of Collection 10 (now in Ruby Valley Indian Reservation), were also fishless.

Collection 11 (figs. 8, 12, 14, 49). Head of Odgers Creek (headwater of Butte Creek), 0.8 to 1.2 km. below source (Sheep Corral Springs, ca. 1.6 km. north of the then fishless Twin Springs), in Sec. 28 and 29, T. 27 N., R. 62 E.; Elko County, ca. 7.2 km. north of White Pine County. Very clear water, but very easily roiled to dense chalky-white; rather firm clay and gravel; swift, with pools; moderate vegetation (dwarf *Chara*, moss, etc.); 12° C. at source (air 16°). Hubbs family, June 27, 1942 (H42–46); UMMZ 141517 (205, 24–77 mm.); 6-foot woven-mesh seine.

Populations of that part of Butte Valley formerly tributary to Pluvial Lake Gale. Four Collections (12–15), comprising 766 specimens, well represent the species in the spring-water area, about 11 km. long, at the north end of the part of Butte Valley, Nevada, that drained into pluvial Lake Gale (thence into Lake Franklin). This area probably comprises the total habitat of native fish within the Lake Gale drainage. This conclusion stems not only from our field work, but also from the direct and definite testimony of Jerome Phalan Stratton (mentioned above), who specified as fishless Snow Creek on Gibson Ranch (in T. 25 S., R. 62 E.) and Youngs Ranch, both in the very arid southern section of Butte Valley.

Collection 12 (figs. 8, 12, 14, 49). Spring on Stratton Ranch (see Collection 14); Elko County, 1.6 km. north of White Pine County. Sandy to muddy bottom; depth to ca. 1 m.; moderate current; dense vegetation; 18° C. (air 15.5°). J. E. Deacon and M. B. Rheuben, September 13, 1964 (JED 64–52); UNLV (67, 19–81 mm.).

Collection 13 (figs. 8, 12, 14, 49). Wrights Spring, ca. 1.6 km. west of Stratton Ranch, in same township (T. 26 N., R. 62 E.); barely on Elko County side of Elko–White Pine county border. Moderately clear water

but easily roiled to whitish; rather soft clay-mud; slight to moderate current; some *Potamogeton*, cf. *P. pectinatus*; 18° C. (air 13°). Hubbs family, June 26, 1942 (H42–45); UMMZ 141516 (97, 27–64 mm.); 6-foot woven-mesh seine.

The minnows apparently occurred along only ca. 30 m. of this streamlet, which then formed a wet meadow; the upper 0.4 km. (in Elko County), which was shallow, swift, and partly filled with *Chara* and *Nasturtium*, was apparently fishless, as at Owens Ranch (Collection 15). The discharges from Collections 13, 14, and 15 were reported to remain unconnected, but it seemed probable that they are separated only by more or less meadow-like areas which could be flooded by occasional torrential rains.

Collection 14 (figs. 8, 12, 14, 49). Spring creek, 0.8 km. below springs (Collection 12), on Stratton Ranch, near center of T. 26 N., R. 62 E.; White Pine County, adjacent to Elko County. Clear water, of good quality; firm soil; moderate current; bur-reeds in and along water; 15° C. (air 13°). Hubbs family, June 26, 1942 (H42–44); UMMZ 141515 (383, 11–72 mm.); nearly all taken in one 20-foot haul with a 6-foot woven-mesh seine; including some young taken in meadow about 1.6 km. farther downstream where ditch is broader and largely choked with *Chara*, etc.; resident said young appeared here every year, although entire meadow freezes in winter, and that minnows also occur in sump against hills to southwest. Carp (*Cyprinus carpio*) and, reportedly, trout (*Salmo* or *Salvelinus*) also occurred.

Collection 15 (figs. 8, 12, 14, 49). Spring creek on Owens Ranch, 5 km. southwest of Stratton Ranch (Collections 12 and 14), in SW ¼ of T. 26 N., R. 62 E.; White Pine County, ca. 2.4 km. south of Elko County. Moderately clear water, but easily roiled to chalky-mud color, of good quality; soft to firm alkali clay; moderate to slow current; much *Potamogeton*, cf. *P. pectinatus*, sedges, etc.; 16° C. (air 19°). Hubbs family, June 24, 1942 (H42–43); UMMZ 141513 (219, 25–72 mm.); 6-foot woven-mesh seine. In the half kilometer between collection and head springs, the feeders, swift and with *Nasturtium*, were avoided by the fish.

Populations of Goshute Valley, in former drainage basin of Pluvial Lake Waring. For a number of reasons we find it rather arbitrary and unsatisfactory to separate Goshute and Steptoe valleys, Nevada, for the groupings of Collections of *Relictus*. One reason is that the springs in the northern end of Steptoe Valley, as customarily mapped, drain into Goshute Valley. There is no complete agreement on where the line dividing the two valleys crosses the common graben (as noted on p. 43).

We treat this common graben as comprising the basins of two pluvial lakes, Waring and Steptoe, while realizing that in Pleistocene time the two basins constituted a hydrographic unit, and may still be hydrographically connected in extreme flood.

Four Collections (16–19), comprising 1,246 specimens, represent the populations of *Relictus* that were found to occupy the disjunct spring-fed streamlets of the northern part of the Goshute–Steptoe valley complex below the basin of pluvial Lake Steptoe. We have found evidence of the occurrence here of this dace (and of any native fish) at only three locations: (1) the many springs on Johnson Ranch, where two Collections were made, near the north end of the valley (at the north end of the range of the species); (2) Phalan Creek, 72 arid kilometers to the south-southwest, the western tributary of Nelson Creek, which is the watercourse of the southwestern arm of Goshute Valley; and (3) the springs and ditches just south of Currie, in the stream course formerly followed by the river that connected Lake Steptoe with Lake Waring, 8–16 km. southeast of Phalan Creek.

It seems probable that we have samples from all of the presently fish-inhabited areas in the pluvial drainage basin of Lake Waring below the outlet of pluvial Lake Steptoe near Currie. The one other site shown as plausible on maps, that of Flower Lake (local usage) or Flowery Lake (as mapped), which is near the center of T. 33 N., R. 66 E., on the old lake bed, appeared from an examination on June 23, 1942, to be fishless, and it was so reported by experienced local folk. Although in the spring runoff of 1934 the playa of Goshute Valley had by reports been covered by water, very little remained of "Flowery Lake": one spring-fed pond, covering about 12 × 18 m.

and 0.3 m. deep in center, was choked with *Chara* and other vegetation; and, ca. 0.4 km. north a chain of small knoll springs watered a wet meadow (see also p. 54). There are no indications that any sizable lake has existed in the area of "Flowery Lake." The Gibbes' map of 1873 (p. 8) merely notes at its location "Spring with grass."

We regard it as certain that *Relictus* was native in this drainage area. We secured no historical confirmation for Johnson Ranch (Collections 16 and 17), but did for the two other Collections (18 and 19).

Collection 16 (fig. 12). Meadow springs on Johnson Ranch, east and north of ranch house, near north end of valley, on west margin, ca. 8 km. south-southwest of Oasis, in Sec. 29, T. 36 N., R. 66 E.; Elko County. Moderately clear water (bottom visibility about 1.5 m.); firm clay around bulrushes, to extremely soft in deeper water; slight outflow from each spring; some choked with, or margined by, vegetation (mostly rushes or *Nasturtium*; one with much *Utricularia*; some with *Potamogeton*, cf. *P. pectinatus*; much algae in others), but others more open; uniformly 16° C. in all large springs with flowing outlets, but 21° in one spring without discharge (air 18° in early morning). Hubbs family, June 22–23, 1942 (H42–42); UMMZ 141511-12 (171, 7–99 mm.); dip-net, 6-foot woven-mesh seine, and 25-foot seine with ¼-inch square mesh in bag.

Waste water from the springs on Johnson Ranch flowed (as Hardy Creek) several kilometers southward in a gully, but by 1942 did not provide suitable habitat for *Relictus*. The meadowy spring area was unusually extensive: in the main group, near ranch house, there were 57 fenced springs and others not fenced, and about 1.6 km. north there were 15 or 20 other springs. The outlet of the one alluvial-slope spring (Collection 17) flowed along the south margin of the meadow—a point pertinent to the finding that the fish from the meadow springs have on the average deeper bodies and wider heads than those from the upper spring, although those from both habitats reach an unusually large size for the species (p. 214). Originally, before modification by ranching, the springs here probably produced a large area presumably occupied by the relict dace in large numbers. The Gibbes' map of 1873 (p. 8) shows a cluster of "Large Springs" with outlet leading south about 18 km., with label alongside noting "Good Grass" (indication of a meadow, where stream course is now entrenched).

Collection 17 (fig. 12). Alluvial-slope spring, just south of house on Johnson Ranch, and just above meadow springs (Collection 16). Very clear water of excellent taste; firm to soft clay and sand; moderately fast current; much *Potamogeton*, cf. *P. pectinatus*, and algae, and lined with *Nasturtium*; 21° C. (air in afternoon 27°). Hubbs family, June 22–23, 1942 (H42–41); UMMZ 141509–10 (706, 16–114 mm.); 6-foot woven-mesh seine, and 15-foot seine with ¼-inch mesh. Fish abounded (one two-quart jar was filled by one haul of the 15-foot seine). Some were exceptionally large (fig. 51).

Collection 18 (figs. 8, 12). Outlet ditch of large spring (mapped as "Twin Springs"), on edge of Phalan Creek 3.2 km. above (west of) house of Phalan Ranch ("Phalen Creek Ranch" on many maps),[4] ca. 11 km. northwest of Currie, near southeast corner of T. 29 N., R. 63 E., Elko County. Phalan Creek is the upper, western tributary of Nelson Creek, the main watercourse of the southwestern arm of Goshute Valley. Clear water, but easily roiled; mud and a little gravel, generally firm, with some stony marl; slight to swift, mostly moderate current; generally dense vegetation (*Nasturtium*, *Chara*, and *Potamogeton*, cf. *P. pectinatus*); 21° C. (air 29°). Hubbs family, August 25, 1938 (M38–165); UMMZ 124966 (168, 26–93 mm.); 6-foot woven-mesh seine.

Mrs. Zubiri, whose other testimony is mentioned on p. 206, reported in 1938 that she found minnows common here as a girl, which would have been about 1902 or 1903. Some years prior to our conversation she saw minnows at the site of Collection 19.

Collection 19 (figs. 8, 12, 14). Large springs in narrows of valley, about 3 km. south of Currie, and upper 1.6 km. of outlet ditch toward Currie, on either side of the T. 27–28 N. boundary, at middle of R. 64 E. (ca. 40° 15′ N. lat., 114° 45′ W. long.); Elko County. Clear water; sand, clay, peat, and gravel; slight to swift current; much *Chara*, *Nasturtium*, and *Potamogeton*; 19 C. (air 31°). Hubbs family, August 24, 1938 (M38–164); UMMZ 124963 (201, 23–87 mm.); 6-foot woven-mesh seine.

[4] Jerome Phalan Stratton, Road Supervisor of White Pine County, informed us at Ely, on June 25, 1942, that the proper spelling is Phalan ("grandmother Phalan brought me into the world")

These springs are at the junction of intermittent McDermitt Creek ("Williams Cr." on some maps) with the lava-entrenched canyon through which ancient Lake Steptoe discharged into Lake Waring.

Already in 1938 evidence existed of the depletion of *Relictus* in this area. The storekeeper at Currie reported that minnows were formerly common from the spring meadows to the road bridge in town (though not above the meadows); and that years previous Mr. Zubiri had caught minnows here in a burlap sack for bait. On September 13, 1934, during a cold night, Hubbs on examining the stream from Currie to and including the headwater springs and ponds located no minnows, though presumably at least a few were present. In 1938 he found the chubs only in the upper 1.6 km. of the stream, chiefly in quieter, deeper, weedier sections retaining a semblance of natural condition. Obvious factors in the depletion had been the straightening of the formerly tortuous stream course, accelerating the current; repeated cleaning out of the aquatic vegetation; diversion of the stream into irrigation ditches (we saw trout dying as a result); and stocking of rainbow and brook trout (*Salmo gairdnerii* and *Salvelinus fontinalis*), many of which were seined.

POPULATIONS OF STEPTOE VALLEY, IN FORMER DRAINAGE BASIN OF PLUVIAL LAKE STEPTOE. Ten Collections (20–29), comprising 2,324 specimens, rather adequately represent the populations of *Relictus* occurring in Steptoe Valley, Nevada, above the stream connection between ancient lakes Steptoe and Waring. The stations cover a north-south space of about 100 km., probably enclosing nearly all of the habitats in this valley for the relict dace. The hydrography of the basin has been treated by Eakin *et al.* (1967). The most plausible additional habitat suggested by examining the relatively recent topographic maps is the cluster of springs shown in the Willow Creek basin near the western base of the Egan Range, but an examination in 1969 of these waters, as well as of other places in the drainage basin of pluvial Upper Lake Steptoe, disclosed no trace of native fish (pp. 59–60).

Evidence that *Relictus* has long existed in Steptoe Valley despite the introduction of trout and other exotic fishes and despite other vicissitudes of existence, and that it is almost certainly native here, has been provided, for most of the Collections (21–26), by long-time residents, including John Yelland, who had come into Steptoe Valley in 1881 and, when still observant and well preserved, was interviewed by us in Ely on August 22, 1938.

Collection 20 (figs. 8, 12, 14). Spring runs on Cardano Ranch, on west side of valley between towns of Cherry Creek and Currie, in Sec. 5, T. 25 N., R. 64 E.; White Pine County, about 7.2 km. south of Elko County. Water clear, but easily roiled; firm to rather soft clay, mud, and a little gravel, with some stony marl; current none to slight; generally choked with *Nasturtium*, *Chara*, *Potamogeton*, cf. *P. pectinatus*, *Hippurus*, and filamentous algae; 14° C. (air 33°). Hubbs family, August 24, 1938 (M38–162); UMMZ 124962 (257, 17–93 mm.); 6-foot woven-mesh seine. Local testimony in 1938 indicated that bass (presumably *Micropterus salmoides*) had occurred in the pond on this ranch.

Collection 21 (figs. 8, 14). Slough at Warm Springs (railroad station), near Monte Neva Hot Springs, about 37 km. north of Ely, in Sec. 25, T. 21 N., R. 63 E., White Pine County. Firm mud and gravel bottom, becoming mud near banks; no current; 21° C. J. E. Deacon, K. Larsen, and J. Tener, June 27, 1962 (JED 62–27, in part); UNLV 175 (147, 12–42 mm.). John Yelland testified in 1938 that minnows had been here since the early 1888's.

Collection 22 (figs. 8, 14). Spring and outlet on Campbell Ranch (Steptoe P. O.), on west slope of valley 32 km. north of Ely and 19 km. northwest of McGill, in Sec. 5, T. 19 N., R. 63 E., White Pine County. Clear water; mud, gravel, ledges of spring deposits, etc.; slight to swift current; generally choked with *Nasturtium*, *Chara*, etc.; 24° C. (air 21°). Hubbs family, August 25, 1938 (M38–166); UMMZ 124967–68 (341, 15–87 mm.); 6-foot woven-mesh seine. Many carp (*Cyprinus carpio*), and goldfish (*Carassius auratus*), and some hybrids between them, were also caught. The head reservoir, about 7 × 15 m., had just been washed out.

Mr. Campbell, then 57 years old, the son of the man who settled the ranch in 1878, felt sure that the minnows are native on the ranch, and

other "old-timers" confirmed the occurrence of minnows here long ago. Campbell claimed that before the great smelter at McGill modified conditions deleteriously, the minnows abounded in the "Slough" (mapped as Duck Cr.) below the ranch, to the extent that wagon loads could be gathered when the holes went dry in summer. John Yelland confirmed the evidence that minnows had been common on this ranch since the early 1880's.

Collection 23 (figs. 8, 14). Springs on Steptoe Ranch (same location as for Collection 22). J. E. Deacon and party, June 27, 1962 (JED 62–27, in part); UNLV 174 (150, 13–41 mm.). The springs still contained carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*) as well as the minnows, indicating that these exotic cyprinids had not excluded the *Relictus* population over a period of more than a quarter century.

Collection 24 (figs. 8, 14). Grass Springs, on Lusetti Ranch, 0.4 km. north of ranch house, on western side of valley about 27 km. north of Ely, draining into a slough in the flood drainage of Duck Creek; in Sec. 20, T. 19 N., R. 63 E.; White Pine County. J. E. Deacon and party, June 27, 1962 (JED 62–27, in part); UNLV 169 (155, 21–63 mm.).

Collection 24 was from one of three separate springs inhabited by this dace. A fourth, larger spring supported only Sacramento perch (*Archoplites interruptus*), but, according to Ellen Vallee, the owner's daughter, it formerly also held minnows.

Collection 25 (figs. 8, 14). Upper spring ditch on Dairy Ranch, just below McGill (below reservoir used as swimming pool), in Sec. 20, T. 18 N., R. 64 E.; White Pine County. Moderately clear water (bottom visibility more than 1.0 m.); gravel and mud, mostly rather firm; uniformly moderate current; rather thick bottom growth of *Potamogeton*, cf. *P. pectinatus*, and considerable floating algae on sides; 25° C. (air 32°). Hubbs family, August 23, 1938 (M38–160); UMMZ 124956–57 (367, 13–81 mm.); 15-foot seine with ¼-inch square mesh.

Goldfish (*Carassius auratus*), originally very brightly and variably colored according to local testimony, but since planting almost totally reverted to wild type, were common here. John Yelland informed us that goldfish had been present for many years, along with minnows, in a deep hole on the Dairy Ranch.

Collection 26 (figs. 8, 14). Several small springs and a little creek on Georgetown Ranch, in meadow just north of railroad yards of East Ely; tributary to Murray (sometimes corrupted to "Murry") Creek (open sewer of Ely, used for irrigation on ranch); in Sec. 2, T. 16 N., R. 63 E.; White Pine County. Clear water; spongy bottom; minute pools and riffles; generally choked with *Nasturtium* and *Potamogeton*, cf. *P. pectinatus*; water cool. Hubbs family and Earl Mangum (local game warden), August 22, 1938 (M38-158); UMMZ 124954 (403, 15–81 mm.); 6-foot woven-mesh seine. The largest spring, on south side of railroad tracks, was reported to have harbored many of the minnows before it was cleaned out and cemented in.

Collection 27 (figs. 8, 14). Ruth Pond, just west of Ruth, in T. 16 N. (near middle of north border), R. 62 E. Collected about 1964 by Dale V. Lockard, of Nevada Fish and Game Department, Wheeler District, Ely (6 specimens, not measured, received from him March 29, 1965, and returned). Probably the dace had been introduced here, well above the usual valley-bottom habitats.

Supplementary Collections near Ely. After the text and maps of this report had been readied for the press, two additional collections of the relict dace have come to our attention. These were collected by Donald R. Cain of the Ely District Office of the U. S. Bureau of Land Management and Frank N. Dodge of the Nevada Department of Fish and Game. The specimens were submitted to Miller for identification. The specimens have been sent to Japan, through Dr. Teruyo Uyeno. The first collection, of 10 specimens, of both sexes, 43–55 mm. long, was taken in Steptoe Creek 1 mile (1.6 km.) south of Ely, on May 24, 1971. The second collection, of 10 specimens, of both sexes, 36–73 mm. long, was collected at Fish Pond Springs, on C–B Ranch, at the same spot as Collections 28 and 29, described below. Mr. Cain raised the question of the possible need for providing a sanctuary under Federal ownership for the protection of the fish at the C–B Ranch, in view of the danger to the fish imposed by irrigation practices and the removal of the aquatic vegetation. Miller had already discussed the

question with James M. Vaughn at C–B Ranch in 1969. A sanctuary here for *Relictus* would indeed be a propitious prospect for the perpetuation of this unique endemic fish.

On July 13, 1972, Robert J. Behnke and Frank N. Dodge collected 14 additional specimens, 31–75 mm. long: a few in Fish Pond Springs, where the dace were very scarce in the spring outflow, registering 13° C., and the rest in a small stagnant pool, with murky water at ca. 27° C., and with tremendous numbers of dace showing no signs of stress. This pool, thought to be in the dry course of Steptoe Creek, was the same one seined by Cain and Dodge on May 24, 1971.

We have recently learned that Thomas P. Lugaski, a student at University of Nevada, Reno, has collected specimens of *Relictus solitarius* in Steptoe Valley and has been studying them.

Collection 28 (figs. 8, 14). Springs on "3 C" or "CCC" (Consolidated Copper Company) Ranch about 1.6 km. north of ranch house, at base of truncated cones close to Steptoe Creek, about 10.5 km. south-southeast of Ely, near Sec. line 5–8, T. 15 N., R. 64 E.; White Pine County. Very clear water, of good taste; firm gravel to extremely soft organic mud; slight to moderately swift, occasionally swift, current; generally choked with vegetation (*Nasturtium*, *Chara*, and *Potamogeton*, cf. *P. pectinatus*); 9° C. (air 27°). Hubbs family, August 23, 1938 (M38–159); UMMZ 124955 (209, 17–89 mm.); 6-foot woven-mesh seine.

Collection 29 (figs. 8, 14). In same springs sampled by Collection 28; shown as Fish Pond Springs on Ely 15-minute and Comins Lake 7.5-minute quadrangles; ranch now named C–B Ranch. Very clear water, but easily muddied; gravel, sand, and deep mud; slight current; dense *Chara*, *Nasturtium*, and *Potamogeton*, cf. *P. pectinatus*; 15° C. (air 27°). Miller family, August 17, 1969 (M69–15); UMMZ 188959 (286, 20–79 mm., plus 3 skeletonized, 70–82 mm., plus some kept alive for chromosome study); 12-foot woven-mesh nylon seine. Clearly the relict dace had maintained abundance here. A more recent Collection at the same place is mentioned above.

ADDITIONAL EVIDENCE ON THE PRESENCE OR ABSENCE OF *RELICTUS* AT SEVERAL LOCALITIES IN STEPTOE VALLEY NOT REPRESENTED BY COLLECTIONS. Green Ranch, west of middle of T. 25 N., R. 64 E. Mrs. Zubiri (née Green), a lady then about 50 years old, told us on August 23, 1938, that there never were minnows on this ranch except once, about 1902 or 1903, when hundreds, dead, appeared on the meadow below after a cloudburst.

Murphy (formerly Dolan) Ranch, in southwestern corner of T. 25 N., R. 64 E. Mrs. Zubiri added that as a girl she caught minnows in a sack in a pasture on this ranch, keeping "the larger ones, about 5 inches long, to eat like sardines." She said that the minnows then swarmed by the thousands in the springs. This statement almost surely reflects the former occurrence here of *Relictus*, although we collected only *Gila atraria*, obviously a recent introduction, probably with trout (p. 58). It is further probable that manipulations to establish bass and trout, including the stocking of Utah chubs, have led to the depletion or elimination of *Relictus* from this spring area, which provides a habitat seemingly normal for this endemic dace.

Cherry Creek vicinity, in T. 23–24 N., R. 62–63 E. This area does not appear to provide proper habitat for *Relictus*, and local testimony in 1938 did not indicate presence of minnows. On June 26, 1942, Cherry Creek flowed intermittently near its mouth but contained no fish. Cherry Creek Hot Springs (45° C.), on alluvial slope 2.1 km. south of Cherry Creek (old town) fed a small reservoir containing goldfish (*Carassius auratus*).

Thirty-mile, Indian, and many other springs on route from Ely to Butte Valley. These are all mountain springs, small and surely without native fish, whereas practically all of the valley-bottom springs in Butte Valley contain minnows, "with no variation," according to Jerome Phalan Stratton and his ranch operator at Stratton Ranch (personal communications, June 25–26, 1942).

Lackawanna Spring, on the western slope of valley 3.2 km. north of East Ely, in the northern part of T. 16 N., R. 63 E. This spring was said in 1938 by local residents William McGill and Earl Mangum to have contained minnows [pre-

sumably *Relictus*] prior to the piping of the water into a bathhouse.

Schell (often 'Shell') Creek and vicinity, in the northern part of T. 22 N., R. 64–65 E., in the Schell (or 'Shell') Creek Range on the east side of this basin. Local testimony, and an examination of Schell Creek on Schellbourne Ranch (usually 'Shellbourne,' and variously otherwise spelled), a long-established and major enterprise, indicated in 1938 and 1942 that there were no fish in the creek or in mountain springs feeding this ranch, and that the only fish in the pond were goldfish, *Carassius auratus* (which John Yelland testified, in 1938, had been there for many years). This small pond, at the ranch, is fed by Lower Schell Creek Spring, which registered a temperature of 26° C. in winter. Upper Schell Creek Spring, about ¾ mile above, is cooler (22° C.), and is diverted for domestic use. This information was furnished in 1971 and 1972 by W. E. Ireland and Robert L. Schultz of the Bureau of Land Management.

The location during exploratory years of Schell Valley is discussed on pages 233–235, for its bearing on the original distribution of *Relictus solitarius*.

Introduced Populations Of Spring Valley, In Former Drainage Basin Of Pluvial Lake Spring

Five Collections (30–34), comprising 1,789 specimens, represent the populations of *Relictus* that we found in Spring Valley, Nevada, the site of pluvial Lake Spring. Some information pertinent to the status of the populations is here included in the habitat descriptions, but the evidence that these populations have been derived through introduction is weighed in a subsequent section (pp. 233–235). The capture at Collection 32 of three suckers, formerly thought to represent an endemic species, but now definitely also attributed to an introduction, is treated below (pp. 229–230).

Collection 30 (figs. 12, 14). Springs adjacent to Spring Valley Creek (apparently a map name), near the northern end of the valley, at ranch about 10 km. north of Seigel Creek Road turnoff, in Sec. 31, T. 23 N., R. 66 E., White Pine County. Bottom of mud and organic ooze; cut banks with sedges growing to edge. J. E. Deacon and party, June 5, 1964 (JED 64–43); UNLV (80, 27–67 mm.). Numerous deep springs here fed several canals that had been dug to a depth of about 1.5 m. and contained abundant populations of the relict dace. About 0.8 km. north, similar springs were found to be fishless. Spring Valley Creek was said by rancher to contain fish when the flow was greater in the spring of the year (see Collections 32–33).

Collection 31 (figs. 12, 14). Duplicate of Collection 30, September 15, 1964 (JED 64–56); UNLV (99, 16–66 mm.).

Collection 32 (figs. 12, 14). Spring streamlet and pools above road crossing, arising in a meadow along the course of the mostly dry Spring Valley Creek, in the northern arm of valley, at Stone House (long a well known structure seen by the senior author in 1915 on the old Lincoln Highway between Schellbourne and Tippetts, but by 1938 only seasonally occupied); in Sec. 17, T. 22 N., R. 66 E.; White Pine County. Rather clear water (until disturbed); rather soft mud; current almost none to slight; dense *Chara*, surface algae, and other plants; 23° C. (air 24°). Hubbs family and Miller, July 6, 1938 (M38–48); UMMZ 124786 (1,073, 14–88 mm.); 6-foot woven-mesh seine and derris root in pool at bridge.

Collection 33 (figs. 12, 14). Same spring. Clear water, but easily muddied; soft mud above firm soil; slight but definite current; dense vegetation (dense beds of *Potamogeton*, cf. *P. pectinatus*, and green algae, with some *Lemna* and *Hippurus*, and a *Scirpus* border); 22° C. (air 27°). Hubbs and Miller families, July 5, 1959 (M59–90); UMMZ 177095 (242, 14–81 mm.; plus 7 skeletons; plus 249, 31–81 mm., in exchange series); 15-foot seine with ¼-inch square mesh.

Collection 34 (fig. 14). Ditch in spring-fed meadow about 0.8 km. east-southeast of the then abandoned Keegan Ranch house on the west side of valley flat in Sec. 12, T. 18 N., R. 66 E.; White Pine County. Clear water; mud bottom; slight current; much vegetation; about 20° C. Miller and Hubbs families, July 5, 1959 (M59–89); UMMZ 177094 (39, 10–22 mm.); dip-nets.

The occurrence here of young dace in the meadow strip on the west side of Spring Valley appears to be attributable to wash-down from Spring Valley Creek, probably in one of the occasional floods (on July 6, 1938, Bert Robison informed us of a flood in this stream course, following the drought of 1934, that had periled barns

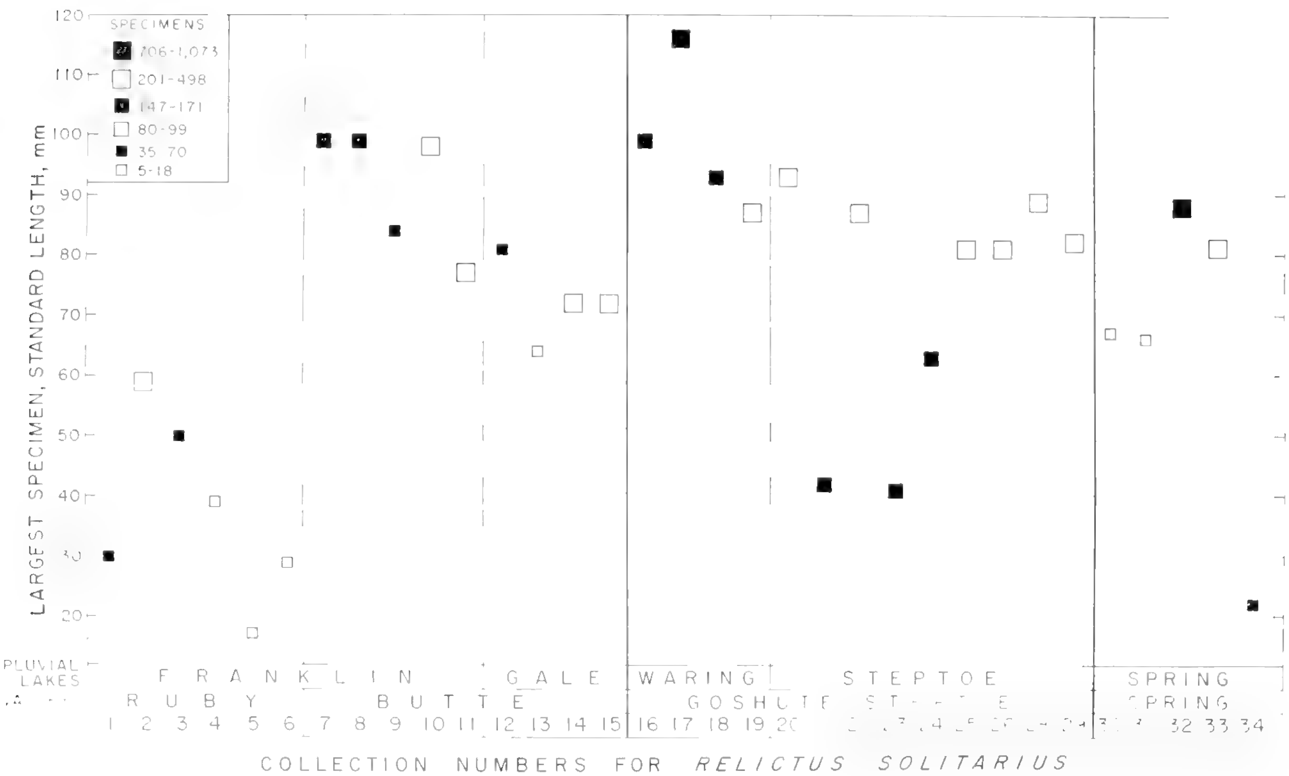


FIGURE 50. Maximum size of specimens in all Collections of *Relictus solitarius*. Data from table 35.

nearby). A half-hour search for other populations in springs and ditches for 0.4 km. below the ranch house disclosed no further populations, and an open, clear, spring-fed ditch below the ranch contained no fish. However, Phil Rowe, who owned the Bassett Ranch about 2.4 km. north, told us that he had seen many small fish in the slough leading to the reservoir below where we collected, and that the fish appear in time of high water. We found the reservoir dry except for one muddy lake.

DESCRIPTION AND COMPARISONS.

Many of the more distinctive features of *Relictus solitarius* are presented in the preceding account of the genus, along with a discussion of the relict status and relationships of the species.

The characters of the species closely simulate those of other spring-inhabiting fishes of the West, such as we have outlined on page 181. These spring isolates are cast into such a similar mold as to obscure their origin, relationships, and classification. As Hubbs and Miller (1948b, pp. 51–52) indicated, this circumstance rendered dubious the generic placement of the species. This doubt persisted until we considered it generically distinct on osteological grounds. Even before that study was made, however, we thought that it probably deserved generic separation from *Rhinichthys*.

SIZE. *Relictus solitarius* is a medium-sized minnow, ordinarily reaching a maximum standard length of 60–100 mm. (table 35; fig. 50), usually larger than *Rhinichthys osculus* but smaller than *Gila bicolor*. Only one of the 34 Collections, no. 17, one of the two at Johnson Ranch in Goshute Valley, contained fish longer than 99 mm., and only 5, among the total of 706 specimens taken there, were larger (101 to 114 mm.), and they look abnormal (fig. 51) and are regarded as superannuated (p. 214). Four other Collections barely missed reaching 100 mm.

(table 35; fig. 50). Specimens longer than 60 mm. are included in all Collections, with the following exceptions: all Collections in Ruby Valley, where the species appears to have been dwarfed (our largest specimen measures 59 mm.); Collections 21, 23, and 34, for which circumstances suggest that the larger adults were not taken; and Collection 27, which contains few specimens, not measured. At least one fish as long as 63 to 99 mm. is contained in 23 other Collections, and at least one longer than 70 mm. occurs in each of these 23 series that contain more than 200 fish, and such a size was attained in each valley, other than Ruby Valley, and in each pluvial drainage basin represented. There is little basis for thinking that markedly different sizes are attained in any of the basins inhabited, other than Ruby Valley, and even there the reduced size indicated for this species may be attributable to environmental conditions, rather than to an inborn characteristic. Predation may have been heavy at times, even primordially, because the spring waters are relatively open and aquatic birds are common during migration. At present, predation by bass is so heavy that limited populations of the dace have survived only in isolated springs. Originally a larger size may have been attained than is indicated by our one main series (Collection 2), for, although local residents had observed only such small fish in the adjacent slough, larger ones, thought (probably wrongly) to have been of a different species, had been seen in certain springs. However, small specimens in Collection 2 had already developed the heavy pigmentation of the adult type, suggesting that indeed the Ruby Valley population was dwarfed, at least when sampled. There is a possibility, albeit seemingly very remote, that another larger minnow, most plausibly *Gila bicolor*, occurred in Ruby Lake prior to its elimination by bass.

COLORATION. The general color tone of half-grown and adult specimens in alcohol, save for the isolated blackened regenerated scales (described below), is ordinarily rendered almost evenly dusky by innumerable melanophores that are arranged without a trace of the concentration around the scale-pocket margins that is usually evident in cyprinids (this lack of scale margining may be attributed to the deep embedding of the scales). The melanophores become sparser ventrally and in some adults (including the holotype) remain undeveloped on the ventral surface of the trunk, whereas many other specimens are puncticulate there.

The melanophores are of two sizes. Small ones are the more numerous, but large ones, as in the subgenus *Siphateles*, typically occur ventrally, and frequently predominate there; and some often occur dorsally. The melanophores that occur exclusively or predominantly on the darkened regenerated scales (see below) are of the larger size. On the silvery opercle, the main part of the cheek, and the exposed part of the shoulder girdle, the larger chromatophores are conspicuous and the smaller ones are few. In contrast, minute melanophores render dusky the region bordering the eye, the entire top of the head including the snout, and also the suborbital region, where, occasionally, a concentration of pigment and a downward extension of the pigmented area simulate a short, oblique subocular bar. The lower, more silvery part of the iris typically bears few, scattered large melanophores and few small ones, whereas the upper part is densely puncticulate with small ones. The dark upper and lower lips and the anterior intergular region become densely punctate in adults, especially in males, leaving largely clear most of the dentary, branchiostegals, posterior intergular, and exposed shoulder-girdle regions. The narial flaps are also puncticulate, especially toward the margin. The biting edges of the lips are clear of pigment, but the floor of the buccal cavity is darkened by melanophores which, in subadults, are few and are restricted to the forward part of the cavity.

There is almost no trace of the lengthwise striping that is typically more or less sharply evident in *Rhinichthys*. In the superficial pigmentation there is no indication of a longitudinal streak on the head, such as *Rhinichthys* characteristically

displays, at least on the snout. Some specimens of *Relictus*, however, show a deep-lying dusky area, without obvious melanophores, below the nostril. Moreover, there is no longitudinal dark band on the body, except, in some specimens, for a deep-lying axial dusky streak, similarly without superficially discernible melanophores. This streak tends to be restricted to the posterior part of the body, and in some Collections, without sharp geographic significance, is rather conspicuous. A special concentration of the black regenerated scales along the midlateral region, presumably resulting from an injury, occasionally presents the impression of an irregular lateral band, or even, rarely, a row of short cross bars. There is tremendous variation in degree and type of speckling due to the irregular loss and regeneration of scales.

The fin bases and the middorsal and midventral lines in the adults are remarkably free from the pigmentary striping that is seen in most American cyprinids. Ordinarily, in *Relictus*, there is the barest, diffuse trace of a darker stripe from dorsal fin to occiput; no especially darkened or clear areas at the origin or midbase of dorsal fin (some smaller adults and subadults do show a somewhat depigmented area about the front of dorsal and some darkening of base medially); and no dorsal-midline intensification of the deep-dusky pigmentation between dorsal and caudal fins. Melanophores are vaguely clustered posteriorly on the lower surface of the caudal peduncle, but do not form there a definitive band or streak, either superficial or deep. About and immediately before the lower procurrent caudal rays there is a small clear area, which is not matched at the dorsal edge. This dace therefore lacks the paired light areas at the caudal base that are ordinarily seen in *Rhinichthys*.

The fins in the adult ordinarily become darkened by numerous melanophores, which tend to be concentrated along the middle of the rays basally but along the margins of the branches of the rays distally. The chromatophores are fewer, and are retarded in development, on the pelvic and anal fins, where they are very few in many subadults and in half-grown fish, and may even be weak or in some localities absent, in some larger adults. These fins are largely clear marginally. The pectoral fin is dark to the margin, except on the inner-ventral part. In development, the membranes of the dorsal fin, the caudal fin (especially on the lobes), and the pectoral fin near its front-upper edge, rapidly become crowded with small melanophores, whereas elsewhere the fin membranes remain largely clear. In these several respects, the mature males tend to assume the adult coloration more rapidly and more fully than do the females.

The peculiar pattern referred to above, caused by irregularly scattered scales that have been blackened by being beset over the entire exposed surface by large melanophores, imparts a *Rhinichthys*-like appearance to *Relictus*, but is not a trustworthy indication of phyletic relationship. The same pattern (Langlois, 1929, p. 161; Hubbs, 1942, p. 5) occurs in other cyprinids. It is a conspicuous feature of the several subspecies of the probably not closely related eastern North American cyprinid now known as *Semotilus margarita* (Cope), which for some time previously was referred to a monotypic genus *Margariscus*. This pattern, occasionally rather conspicuous, but commonly barely evident, is also seen in another probably not intimately related cyprinid, *Couesius plumbeus* (Agassiz), which for some time recently was referred to *Hybopsis* (Bailey *et al.*, 1960, p. 14), but has now been referred again to *Couesius* (by Bailey *et al.*, 1970, p. 19). The same pattern we find to hold for another probably distantly related cyprinid, the peculiar Pacific-drainage minnow *Oregonichthys crameri* (Snyder), which was originally, and again recently (Bailey *et al.*, 1960, p. 14; Bailey *et al.*, 1970, p. 20) referred to *Hybopsis*, but which, according to osteological research by Ted M. Cavender (personal communication, 1970), deserves separation in the distinct genus *Oregonichthys* Schultz and Hubbs (1961); Reno (1969) has also suggested that *Oregonichthys* deserves generic

status, on the basis of the unique structure of its neuromasts. (Similar appearing blackened scales that are conspicuous in two eastern species currently referred to *Hybopsis*, namely *H.* (*Erimystax*) *dissimilis* (Kirtland) and *H.* (*E.*) *x-punctatus* Hubbs and Crowe (1956), are basic elements of the color pattern, unrelated to scale regeneration.)

The peritoneum is silvery, with brown puncticulations.

The pigmentation develops very early. At a standard length of 10–18 mm., as indicated by Collections 1 and 5, the melanophores are already well developed. The middorsal streak has not yet developed, except along middle of dorsal base, where it is black. There is a similar streak along base of anal fin. A fine black streak has developed along the axial septum of the lateral muscles. The dark blotch below the nostril has already become rather conspicuous, but does not form a lengthwise band, such as is seen in corresponding young of *Rhinichthys*.

When a length of 20–25 mm. has been attained (as indicated by Collection 3), a dark, deep-lying, rather diffuse middorsal streak has appeared, more strongly before than behind the dorsal fin. It shows along the middle of the dorsal base, which, however, is pale about the front of the fin. No definite streak has formed behind the anal fin, where some separated melanophores, not evident in smaller fish, have formed. A file of 1–6, usually 2–4, huge melanophores lie along each side of the anal base medially (these are inconspicuous when the pigment granules are centrally concentrated, and in some specimens they appear to be lacking). A deep-lying, diffuse axial streak has appeared about the now weak black axial line. A very irregular dorsolateral file of large melanophores has formed but soon fades. Little pigment has yet developed below the eye.

Life color. The life colors of *Relictus solitarius* were found to be extremely variable, perhaps in correlation with its secretive habits and with reduced selection pressure in its isolated habitats. The colors were described by us in the field for Collections 2, 7, 8, 10, 11, 15–18, 20, 22, 25, 26, 28, 32, and 33 (pp. 199–207), which represent well the geographical range of the species. The life-color variability is another unique feature of the relict dace.

The colors are highly variable individually and to some extent geographically, but with considerable coherence in some respects. The general tone is usually dusky, strongly speckled with brown or, in some localities, with moss-green. In addition to rather bright blue reflections, which are generally apparent, there is more or less gilt, varying individually and regionally from almost none to quite bright. Many possess also a pale to deep tinge of violet (especially noted for Collection 2). Coupled with this, usually, is an exceptionally heavy coating of slime.

At some localities the general color was noted as especially variable. Thus, in Collection 32, the general tone graded from silvery gray, through pale to deep olive, to rather rosy (but never red) or to purplish olive-brown, with reflections from individual scales varying from silvery to bright blue or gilt. Some specimens (as noted for Collection 28) tended to grade toward yellow or gray. In some examples (as recorded for Collection 25), the entire back is rather uniformly pea-green and the mid-sides are either silvery or gilt; other specimens have the sides dappled with bright metallic-green scales; some vary toward olive or gray. In others (as observed in Collection 17), the general tone is usually metallic greenish, bluish, or brassy; some fish (as in Collection 16) are even more variable—silvery, greenish, golden or, often, yellow-tan, and, on the average, definitely more gilt than in some other series. In Collection 15 the various hues on the upper parts ranged from bright brassy green to dark olive or grayish green. The back (as it was in Collection 10) may be bright grassy green.

Generally the lower parts are lighter, often silvery or watery white; or silvery white, usually with a blue tinge; but in some, either the dusky dorsal color (in darker fish, as observed in Col-

lection 18), or the yellowish color, extends over the ventral region. Intervening between the upper and lower sides is a narrow deep-lying dorsolateral stripe that is often pearly or golden (as seen in Collection 17) or bright brassy (Collection 10). The midsides are often largely silvery, with more or less conspicuous reflections of brassy or violet. In very large females (as in Collection 17) considerable gilt may show along a midventral streak on the abdomen, as well as on the side of the body and on the lower fins and their axils.

The lower fins are often yellowish or lemon, occasionally rather bright golden or yellowish (as seen in Collection 32); watery white in others, especially in small females; but never red. The dorsal and caudal fins are usually more or less amber, often suffused with greenish or yellowish, either light or dusky; sometimes dusky gold. The lower fins show, at least in some fish, blackish speckling on the rays and broad blue-gray borders. In some Collections (as observed in Collection 16), all fins may be yellowish, except near the margin.

Many individuals are waxy or watery yellowish or lemon-colored on the pectoral and pelvic axils, but, unlike *Rhinichthys* and some other western minnows, this species never has either axil red, even in breeding males. As observed in some Collections, breeding males may be brighter than females, but none have red fins. Breeding males may have sooty lower fins (as seen in Collection 33).

The opercle and the cheek behind the eye are more or less gilt, but there is no definite bright color bar at front of opercle. Very large specimens (as observed in Collection 18) may be bright blue across the upper edge of the opercle. The iris (as noted for Collection 28) may be golden only on a narrow inner rim, or (as seen in Collection 25) may be bright silver-gilt about pupil and sometimes gilt or orange elsewhere.

One adult (in Collection 25) was so golden that it appeared to be a mutant. Its back was a mixture of green and blackish; the sides were bright, clear golden yellow; the lower fins were a bright and clear, rather intense, golden yellow; the caudal fin was of the same color, with a large blackish blotch on lower lobe and finer blackish marking on the upper lobe. Some other specimens were sufficiently extreme to approach a mutant appearance. In addition to the blackish regenerated scales (which are often concentrated near midsides or toward base of caudal fin to form seemingly aberrant color markings), jet-black blotches occasionally appeared on the body or fins (for example, on front edge of dorsal fin near base in an adult in the type series, Collection 7).

FORM AND GENERAL APPEARANCE. This is a rather chubby fish (fig. 35C,D), which the field notes indicate as relatively soft-bodied. However, it almost invariably preserves well, with very little tendency toward further softening or distortion. The deep imbedding of the scales imparts a fleshy feel to the surface, which tends to be slimy.

The general form is that of a comparatively sluggish midwater swimmer, with rather deep body and deep peduncle, and rounded dorsal and ventral contours which are relatively symmetrical, with the dorsal profile not very much more curved than the ventral. The muzzle is rounded in both the lateral and the dorsal aspect and the rather large, straight, and oblique mouth rises forward, so that the upper lip, which is about even with the lower or only slightly protrudes, is about on the longitudinal axis of the body. It is not a conspicuously streamlined fish. The fins are relatively small and are generally strongly rounded; the paddle-shaped pelvics are particularly distinctive. The fins tend to be very flexible, often rather silky toward the margin. With age, the rays commonly branch more extensively than is usual, so that in many specimens they fan out at the margin to touch one another.

Primarily because of the posterior location of the pelvic, the dorsal origin varies from slightly before to slightly behind the vertical from the pelvic insertion, usually slightly behind. In this respect *Relictus* agrees essentially with *Gila bicolor*, but contrasts with *Rhinichthys*, which has the origin of the dorsal fin behind that of the anal fin.

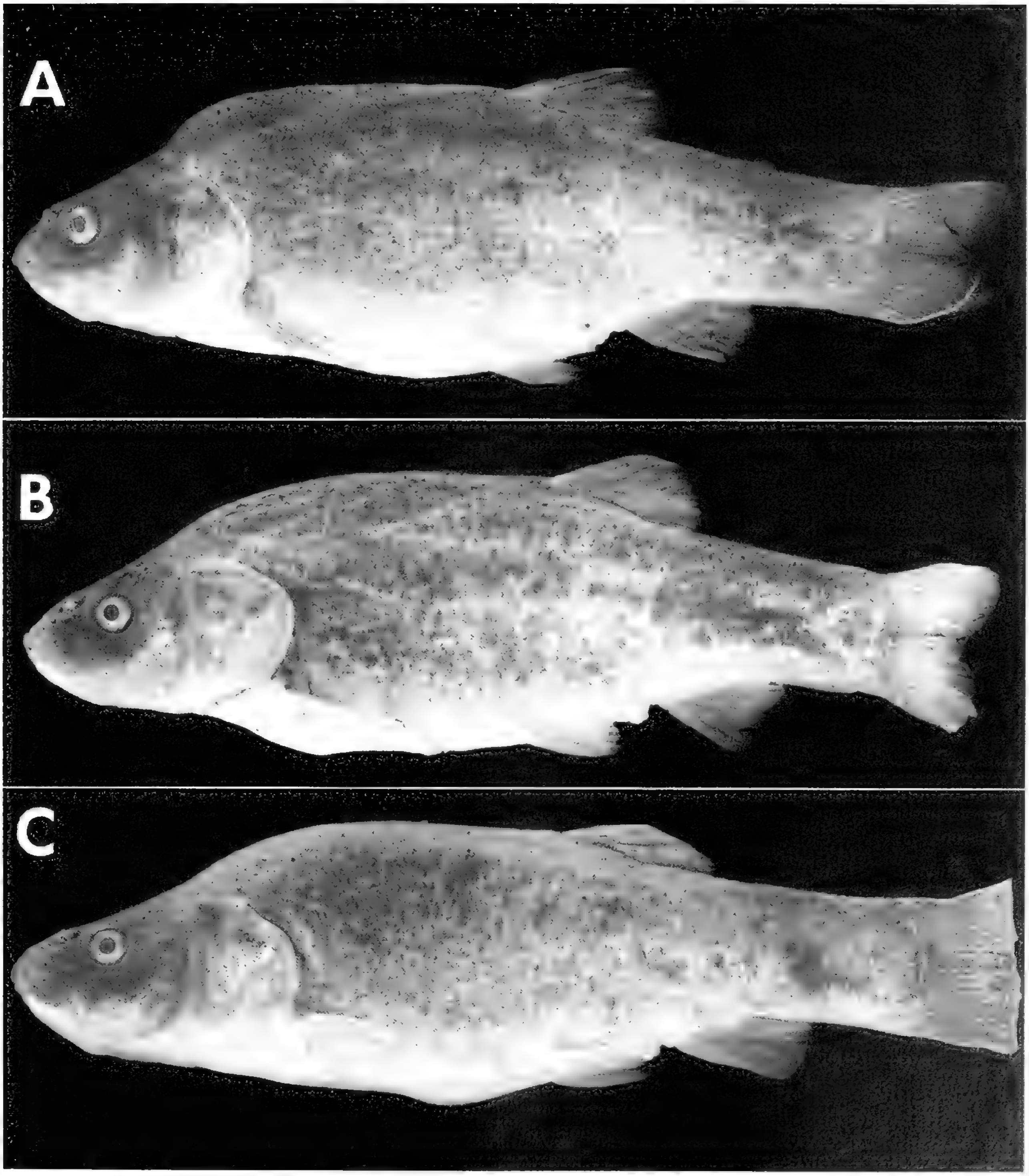


FIGURE 51. *Relictus solitarius*: superannuated females from Johnson Ranch, Goshute Valley, Nevada; Collection 17. A. UMMZ 141510, no. 2, 107 mm. B. UMMZ 141510, no. 4, 114 mm. C. UMMZ 141509, 113 mm

The general appearance of this fish contrasts particularly with that of *Rhinichthys*, though it and some of the most modified of the spring-restricted forms of that genus converge considerably.

Most of the features just mentioned seem to align this fish with *Gila bicolor*, but its duskier color, generally smaller and more imbedded scales, very incomplete lateral line, less regular squamation, much slimier integument, softer flesh, and generally smaller size belittle the resemblance.

In many of the aspects of form this species, in comparison with other western minnows, seems to be unusually variable. Differences in form in addition to those that appear in comparing the measurements are rather notable in several respects. In some specimens the upper profile of the head is more nearly horizontal and is much less decurved anteriorly than in others. This character is usually associated with a large mouth and an especially turgid upper lip, but the correlation is by no means uniform, and this character is highly variable and is far from consistent at any one locality. This modification of the head profile is most strikingly evident in Collection 17, one of the two at Johnson Ranch, far north in Goshute Valley, and is particularly pronounced in the oversized females, of which three are illustrated (fig. 51). Such modification is displayed to some extent in a varying proportion of the specimens in other Collections. There is also some variation (not measured) in the obliquity of the mouth. The width of the opercular membrane also fluctuates considerably.

The modification of form in the few definitely oversized specimens in Collection 17 is extreme but not consistent. They differ among themselves in the robust build, great depth of peduncle, degree of nuchal hump, prominence of muzzle, etc. Such extreme modification of form is commonly seen among oversized fish. Thus, an immense adult female of *Gila orcuttii* (Eigenmann and Eigenmann) that came from a stream into which the species had recently been introduced in northern Santa Barbara County, California had a physiognomy much like that of these huge specimens of *Relictus*.

Lateral-line system. In this species, as in some other minnows inhabiting isolated springs, the lateral line is greatly reduced, often interrupted, and irregular. It rarely extends to below the origin of the dorsal fin, and the part that is developed is often incomplete. In 90 subadult and adult specimens from various parts of the range of the species the pores per side range from 3 to 29, with 68 (76 percent) from 11 to 22, and with the mean at 16.02. The holotype has 17–19 pores, ending 5–10 scale rows before vertical from origin of dorsal fin.

On the head as well, the lateral-line system is deficient in some respects. The supratemporal canal is complete across the occiput in only 4 among 76 specimens examined from various Collections; these four have 6–8 pores. In the 72 specimens (144 sides) found to have the canal medially interrupted (as often in spring-inhabiting isolates), including 27 specimens from Collection 22 (not listed in table 43) that contain the four with the canal complete, the number of pores per lateral segment on either side ranges from 0 to 5, with 92 counts of 3 and 34 counts of 4, and with a mean of 3.42 pores. The preoperculomandibular pores in 222 counts (2 counts per fish) range from 11 to 19, in a rather similar pattern in the several valleys; average, 13.79. The mandibular pores (table 44) in 158 counts (79 specimens) range from 3 to 8, modally 5, with means fluctuating with the valley from 4.93 to 5.61.

Scale structure. The scales (fig. 46B) are more like those of *Rhinichthys* than those of *Gila*, but usually bear even more numerous radii on all fields. Typically they are vertically oval, with the focus definitely nearer the base than the posterior margin; but, with increasing size, the scales in some individuals (sampled above lateral line just before dorsal fin) become longitudinally rectangular with dorsal and ventral edges straight and horizontal, and with the focus even closer to the base. The two types integrade at a single locality.

TABLE 36. *Proportional measurements, in permillage of standard length, for* Relictus solitarius *in different pluvial-lake drainages. For each entry there is given the range, and below this the mean; numbers of specimens for each category and the Collection numbers involved are shown in table 37, or, when fewer were counted, as a subscript.*

	Predorsal length					Anal origin to caudal base				
Sex	Males		Females			Males		Females		
S.L., mm.	24–42(–)	42–66	30–42(–)	42–66(–)	66–114	24–42(–)	42–66	30–42(–)	42–66(–)	66–114
Lake Franklin										
Ruby Valley	534–616	557–588	550–607	566–599	—	307–354	304–351	285–330	292–331	—
	581	574	577	587	—	329	327	301	312	—
Butte Valley	554–594	549–586	545–615	576–619	593–626	278–316	292–330	276–309	270–301	257–307
	573	577	580	596	604	295	311	290	287	286
Lake Waring	570–631	558–634	589–628	581–642	594–688	286–353	310–371	303–345	275–318	264–332
	600	594	604	611	622	326	333	324	303	295
Lake Steptoe	551–613	556–592	553–600	570–636	532–632	301–332	305–361	292–345	280–324	249–325
	571	571	581	602	589	313	329	317	308	297
Lake Spring	564–620	548–596	587–607	582–617	586–626	309–339	299–345	298–329	284–317	288–315
	593	578	595	597	607	322	331	311	301	297
Total range	534–631	548–634	545–628	566–642	532–688	278–354	292–371	276–345	270–331	249–332
Grand average	585	585	588	602	608	320	328	309	303	294
	Body depth					Caudal-peduncle depth				
Lake Franklin										
Ruby Valley	259–290	241–276	265–301	258–291	—	125–146	116–132	121–145	122–144	—
	274	261	285	272	—	137	126	134	131	—
Butte Valley	271–312	258–302	276–347	272–297	243–302	133–159	131–158	119–148	126–153	128–145
	290	281	290	283	277	142	144	130	137	135
Lake Waring	269–322	256–328	272–306	267–320	258–346	129–173	119–171	123–155	111–182	114–158
	293	282	290	291	296	141	143	133	139	133
Lake Steptoe	265–304	248–289	256–289	253–331	248–301	138–153	139–165	123–158	131–164	124–154
	281	269	277	288	276	145	148	145	150	140
Lake Spring	270–310	269–306	245–317	276–333	290–306	137–158	138–168	129–166	150–158	135–158
	285	287	277	295	299	149	153	142	152	148
Total range	259–322	241–328	245–347	253–333	243–346	125–173	116–171	119–166	111–182	114–158
Grand average	284	280	284	287	288	142	144	137	142	137
	Head length					Head depth				
Lake Franklin										
Ruby Valley	279–313	279–290	288–314	290–311	—	202–226	194–223	203–221	198–219	—
	297	285	301	299	—	211	208	213	208	—
Butte Valley	284–305	276–302	279–300	278–309	275–313	199–227	198–222	200–222	199–218	175–213
	297	288	289	294	291	214	208	210	207	200
Lake Waring	279–319	255–327	294–339	271–334	273–341	209–226	191–241	203–233	193–220	192–229
	306	294	313	300	307	217	208	218	208	206
Lake Steptoe	286–323	272–291	289–313	281–316	245–311	200–229	194–213	202–222	192–221	177–221
	302	281	299	294	283	211	205	212	210	203
Lake Spring	306–325	284–311	281–320	298–327	281–336	206–231	202–221	199–223	210–231	203–230
	311	297	307	308	306	222	216	212	219	216
Total range	279–325	255–327	279–339	271–334	245–341	199–231	191–241	199–233	192–231	175–230
Grand average	302	291	302	299	298	215	209	213	210	206

(Table continued on next two pages.)

TABLE 36. CONTINUED.

	Snout length					Orbit length				
Sex	Males		Females			Males		Females		
S.L., mm.	24–42(–)	42–66	30–42(–)	42–66(–)	66–114	24–42(–)	42–66	30–42(–)	42–66(–)	66–114
Lake Franklin										
Ruby Valley	73–91 81	72–81 77	77–87 83	79–88 84	— —	64–92 78	58–75 68	67–79 73	59–72 64	— —
Butte Valley	73–85 77	68–80 74	65–77 73	72–87 79	70–95 79	62–81 70	59–73 65	64–81 70	59–72 63	46–59 52
Lake Waring	75–89 83	64–92 80	65–90 86	70–104 85	68–103 89	66–93 78	52–75 66	70–90 78	49–76 62	43–66 54
Lake Steptoe	79–92 85	76–87 82	79–90 85	77–93 85	73–97 85	65–77 70	55–68 61	61–70 64	51–65 57	44–59 50
Lake Spring	78–89 83	74–87 82	81–92 86	79–94 86	80–96 88	67–81 74	61–72 65	67–90 78	57–67 62	51–63 56
Total range	73–92	64–92	65–92	70–104	68–103	62–93	52–75	61–90	49–76	43–66
Grand average	82	79	83	84	86	75	65	73	61	53
	Upper-jaw length					Mandible length				
Lake Franklin										
Ruby Valley	79–91 85	74–87 81	82–88 85	79–95 86	— —	98–122 109	94–109 103	101–116 110	106–121 110	— —
Butte Valley	68–90 80	65–89 81	71–86 79	83–88 85	78–94 88	89–114 105	102–113 108	104–112 107	102–113 108	97–116 108
Lake Waring	78–94 84	67–102 83	79–97 88	72–97 85	75–112 94	100–121 113	87–126 108	106–132 117	94–124 110	91–130 114
Lake Steptoe	69–88 80	74–87 79	72–85 80	73–100 86	75–106 87	99–119 110	95–114 104	97–122 107	100–122 108	88–122 102
Lake Spring	81–99 89	71–85 81	74–95 85	77–94 85	87–109 92	105–126 114	99–115 108	99–122 110	99–119 109	99–122 109
Total range	68–99	65–102	71–97	72–100	75–112	89–126	87–126	97–132	94–124	88–130
Grand average	84	82	83	85	91	110	107	110	109	109
	Interorbital width					Suborbital width				
Lake Franklin										
Ruby Valley	91–108 97	89–99 94	92–107 101	97–105 101	— —	33–46 40	41–44 42	36–47 42	40–47 44	— —
Butte Valley	82–100 93	83–101 90	86–94 90	89–103 93	76–99 88	32–44 39	34–42 39	33–49 38	36–46 41	36–51 45
Lake Waring	93–114 104	80–112 95	97–117 109	85–120 101	82–113 97	35–54 40	32–48 40	36–53 44	36–48 42	38–59 48
Lake Steptoe	94–107 101	88–102 95	93–105 97	87–104 97	85–103 96	39–49 44	42–49 45	39–48 43	40–55 45	38–55 46
Lake Spring	90–105 97	85–114 100	84–120 105	93–117 105	99–115 106	35–46 39	37–45 42	37–46 41	39–52 43	38–48 45
Total range	82–114	80–114	84–120	85–120	76–115	32–54	32–49	33–53	36–55	36–59
Grand average	99	95	100	100	97	40	41	42	43	47

(Table concluded on next page.)

TABLE 36. CONTINUED.

	Depressed dorsal fin					Caudal-fin length				
Sex	Males		Females			Males		Females		
S.L., mm.	24–42(–)	42–66	30–42(–)	42–66(–)	66–114	24–42(–)	42–66	30–42(–)	42–66(–)	66–114
Lake Franklin										
Ruby Valley	204–245 238	238–247 242	207–237 221	186–216 205	— —	240–284 261_{16}	261 261_{1}	247–277 261_{7}	234–253 242_{10}	— —
Butte Valley	233–274 257	223–264 245	196–243 220_{9}	185–228 211	182–207 194	233–282 259_{9}	225–273 249	226–247 239_{5}	208–252 236_{9}	209–249 234
Lake Waring	220–263 245	206–277 234	195–246 215	173–227 202	159–210 188_{33}	223–276 247_{13}	209–257 235_{25}	218–253 239_{8}	202–252 228_{27}	178–246 209_{32}
Lake Steptoe	220–244 230[1]	216–271 242_{7}	203–235 218	194–229 207_{16}	170–216 198	216–263 244_{4}[1]	225–255 240_{6}	214–260 238_{9}	210–279 234_{10}	192–231 217_{10}
Lake Spring	228–281 250	240–273 252	205–245 218	189–219 206_{9}	177–213 199_{10}	226–263 245_{7}	224–266 240_{9}	212–251 238_{6}	224–241 232	203–249 227
Total range	204–281	206–277	195–246	173–229	159–216	216–284	209–273	212–277	202–279	178–249
Grand average	243	240_{70}	218_{40}	205_{75}	193_{75}	253_{49}	239_{61}	243_{35}	233_{72}	218_{71}
	Pectoral-fin length					Pelvic-fin length				
Lake Franklin										
Ruby Valley	166–245 211	202–226 213	157–192 176	170–181 176_{10}	— —	138–175 158	152–171 163	127–152 137	122–140 132	— —
Butte Valley	203–236 219	208–242 223	150–213 175	151–199 178	163–188 177	156–185 170	155–194 168	115–164 137	137–175 155	123–139 131
Lake Waring	194–264 222	188–242 215	163–187 178_{9}	143–210 181	147–190 170_{33}	147–183 167	146–190 163	119–151 136	106–169 137	107–151 129_{33}
Lake Steptoe	164–187 176[1]	187–232 209	160–191 174	167–197 182	144–210 175	132–146 138[1]	143–188 167	116–146 134	130–148 139	114–148 133
Lake Spring	169–247 217	199–252 228	156–190 172	168–195 181	155–191 179	130–194 166	157–190 174	125–145 136	125–145 138	121–154 135
Total range	164–264	187–252	150–213	143–210	144–210	130–194	143–194	115–164	106–175	107–154
Grand average	211	218	175_{18}	180_{76}	174_{76}	160	166	136	139	131_{76}

[1] The lengths of the fins in this series are low, because the specimens are only 27–37 mm. long, and had presumably not yet developed the longer fins characteristic of adults.

MORPHOMETRY. A total of 342 specimens were subjected to 18 measurements, including standard length (tables 36, 37). A total of 98 were from the basin of pluvial Lake Franklin, 43 from Collection 2 in Ruby Valley, to represent the dwarf population, and 55 from two Collections (7, 10) in Butte Valley (all those measured from Butte Valley came from below the Lake Gale basin). From the area of the direct tributaries to pluvial Lake Waring 128 were utilized, from four Collections (16–19), including 60 from Collection 17, which contained the grotesque oversized females (fig. 51). From the drainage basin of Lake Steptoe 65 specimens were measured from Collections 20, 22, 25, and 26. From Spring Valley, into which it is held that the species was introduced, 51 specimens were utilized, all from Collection 32. These series were selected to provide a cross-section of potential variates throughout the range of the species (table 37). The specimens were further selected to represent the smaller males, 24 to 42– mm. in standard length (67 specimens); the larger males, 42 to 66 mm. long (71); the smallest females, 30 to

TABLE 37. *Material of* Relictus solitarius *utilized for proportional measurements.*

Pluvial lake	Franklin			Waring				Steptoe					Spring	
Valley	Ruby	Butte		Goshute				Steptoe					Spring	Total
Collection No.	2	7	10	16	17	18	19	20	22	25	26	28	32	Number
Males														
24–42 – mm.	19	10	—	6	10	1	—	—	—	—	10	—	11	67
42–66 mm.	3	13	—	10	18	9	—	—	—	—	8	—	10	71
Females														
30–42 – mm.	10	10	—	4	7	—	—	—	—	—	10	—	9	50
42–66 – mm.	11	9	1	9	10	7	3	1	6	3	5	2	10	77
66–114 mm.	—	8	4	11	15	6	2	4	4	2	2	8	11	77
Totals	43	50	5	40	60	23	5	5	10	5	35	10	51	342

42– mm. long (50); the medium-sized females, 42 to 66– mm. long (77); and the largest females, 66 to 114 mm. long (77). The two sexes and the five size groupings were thus well represented.

Because the relict dace rather surprisingly tends to preserve very soundly and with little distortion by opisthotonus or otherwise, and because large series were obtained, it has been feasible to select, from each Collection utilized, specimens well suited for precise measurement. Furthermore, the material is highly comparable, because of similar methods and length of preservation, and because all the measurements were made by one of us (C.L.H.).

The measurements for each of five body parts, seven head parts, and four fins were transformed into permillage of standard length, and for each size group of each collection the ranges and means were computed. These ranges and means have been tabulated for each of the pluvial lake drainage basins, with the Ruby Valley and Butte Valley sections of the Lake Franklin watershed separated. Five zoogeographical divisions were thus obtained, plus another for the total range and grand average for each size-group category (table 36, which omits the head-width proportions, which are subject to error and would add little or nothing to the picture).

In an effort to determine whether there are important differences in morphology between the populations from the two pluvial drainage systems, or between the populations within either or both systems, individual localities were compared, and smaller size groupings were tried. Little advantage was realized from either refinement. In addition, untransformed measurements were plotted against the standard length. For Collections 16 and 17, lines were fitted by eye to indicate the changes with increasing size of fish. Then the measurements for other Collections were plotted against those lines. This was done chiefly for Collection 2, the main one from Ruby Valley, which seems to be one of the more distinctive, and is dwarfed. For predorsal length, head length, mandible length, and caudal-peduncle depth, the proportions for Ruby Valley are low, but the higher values roughly match the mean line for Collections 16 and 17. The caudal-fin measurements are high for the Ruby Valley lot, but the low values approximate the mean for those Collections. These differences are perhaps largely relatable to the dwarfing of the Ruby Valley fish (p. 209) and to the tendency for exuberant development at Johnson Ranch, particularly at Collection 17 (pp. 208, 214). In any event, the differentiation does not appear to have reached a level indicative of the subspecies distinction. The graphs have been retained, but are not herein reproduced.

Somewhat the same degree of difference and overlap appears when the proportions are compared by ranges and means, for the data compiled by lake basins and valleys (table 36). The differences appear to be about as great within as

TABLE 38. *Size frequencies by sex and maturity in five representative Collections of* Relictus solitarius.

Pluvial lake system Valley (Coll. No.) (Date)	Sex[1]	Standard lengths by two units of 0.5-cm. size classes: 1.5	2.0 + 2.5	3.0 + 3.5	4.0 + 4.5	5.0 + 5.5	6.0 + 6.5	7.0 + 7.5	8.0 + 8.5	9.0 + 9.5	10.0 + 10.5	11.0 + 11.5
Lake Franklin	Yg. ♂+♀	4	27	—	—	—	—	—	—	—	—	—
	Imm. ♂	—	17	2	—	—	—	—	—	—	—	—
Ruby (2)	Imm. ♀	—	32	4	—	—	—	—	—	—	—	—
(Sept. 12)	Ad. ♂	—	5	65	30		—	—	—	—	—	
	Ad. ♀	—	—	23	99	9	1	—	—	—		—
Butte (7)[2]	Ad. ♂	—	—	22	33	15	4	—	—	—	—	—
(June 27)	Ad. ♀	—	—	4	22	14	10	22	11	8	1	—
	Imm. ♂	1	1	4	1	—	—	—	—	—	—	—
Lake Waring (17)	Imm. ♀	2	2	13	2	—	—	—	—	—	—	—
(June 22–23)	Ad. ♂	—	—	119	192	22	—	—	—	—		
	Ad. ♀	—	—	62	147	87	21	10	2	2	3	2
	Yg. ♂+♀	10	—	—	—	—	—	—	—		—	
Lake Steptoe (25)	Imm. ♂	2	71	4	—	—	—	—	—	—	—	—
(Aug. 23)	Imm. ♀	1	36	7	1	—		—	—	—	—	—
	Ad. ♂	—	—	2	46	5	—		—	—		—
	Ad. ♀	—	—	—	17	130	25	8	1	—	—	—
	Imm. ♂	—	1	13	—	—	—	—	—	—	—	—
Lake Spring (32)[3]	Imm. ♀	—	6	22	—	—	—	—	—			
(July 6)	Ad. ♂	—	—	48	39	5		—	—	—	—	—
	Ad. ♀	—	—	26	32	75	52	22	2	—	—	—

[1] Unless sex and maturity was obvious by inspection of sexually dimorphic characters, gonads were examined. The distinction between immature and maturing is somewhat tenuous and probably not wholly consistent

[2] This collection also included an apparent intersex (labelled no 16), 63 mm. long

[3] This collection also included an apparent intersex, 53 mm. long.

between the two main pluvial drainage complexes. In general, the deviation of any mean value for any dimension from the grand average for the species is relatively slight, in comparison with the wide range for the pertinent sex and size group.

SEXUAL DIMORPHISM AND NUPTIAL CHARACTERS. One of the remarkable features of *Relictus solitarius* is the marked discrepancy in the average and the maximum size of the sexes. This has been evident from casual examination of the Collections in general, and is illustrated by the sizes of the specimens subjected to proportional measurements (tables 36, 37). The discrepancy in size is documented by an analysis, according to sex and maturity, of all specimens in five representative Collections (tables 38, 39): Collection 2 for the Ruby Valley and Collection 7 for the Butte Valley divisions of the drainage basin of pluvial Lake Franklin, Collection 17 for the Goshute Valley and Collection 25 for the Steptoe Valley sections of the drainage basin of Lake Waring, respectively, and Collection 32 for Spring Valley. Among these five Collections, the values for the males, expressed in percentage of the value for the females, ranges for the mean size from 90 to 100 for the immature fish and from 68 to 86 for the mature ones. The corresponding values for the maximum size were little altered for the immature fish (86 to 100), but diverged notably for the mature ones, from 49 to 76. The lowest value is for Collection 17, in which the sex ratio is equal; the highest value is for the dwarfed Collection 2 (table 39). The data for the same five Collections tallied by units of two 0.5-mm. size classes (table 38) clearly confirm the larger size of the females. In Collection 2, among 232 maturing fish, the largest male measures only 44 mm. and the largest female only 58 mm. In the four Collections of less dwarfed fish, among which

TABLE 39. *Number and size, by sex and maturity, of specimens in five representative Collections of* Relictus solitarius.[1]

Pluvial lake system Valley (Coll. no.) (Date)		Standard length, mm.[2] Unsexed very young Min.-max. (mean$_N$)	Immature Min.-max. (mean$_N$)	Adults Min.-max. (mean$_N$)	Mean SL♂/Mean SL♀ × 100 Imm.	Adult	Max. SL♂/Max. SL♀ × 100 Imm.	Adult	Sex ratio, x♂:100♀ Imm.	Adult
Lake Franklin										
Ruby (2) (Sept. 12)	Male	15–22(19.4$_{31}$)	23–28(25.5$_{19}$)	24–44(35.7$_{106}$)	100	86	100	76	53	76
	Female		23–28(25.6$_{36}$)	30–58(41.7$_{172}$)						
Butte (7) (June 27)	Male	—	—	33–66(42.8$_{71}$)	—	68	—	67	—	80
	Female			33–99(62.5$_{42}$)						
Lake Waring (17) (June 22–23)	Male	—	17–38(29.3$_7$)	29–56(39.9[illegible])	90	85	95	49	37	99
	Female		15–40(32.6$_{19}$)	30–114(46.9$_{330}$)						
Lake Steptoe (25) (Aug. 23)	Male	13–17(15.0$_{10}$)	17–36(21.9$_{77}$)	34–51(42.8[illegible])	92	79	86	64	173	29
	Female		17–42(23.6$_{45}$)	38–80(54.4$_{154}$)						
Lake Spring (32) (July 6)	Male	—	25–32(29.3$_{11}$)	28–53(37.8[illegible])	99	71	86	62	50	44
	Female		21–37(29.6$_{28}$)	29–86(53.6$_{256}$)						

[1] Frequencies by two units of 0.5-cm. class are entered in table 38; subscript figures denote number of specimens.
[2] Means were computed from data grouped by 0.5-cm. classes.

1,370 specimens were all measured, the longest males are only 51 to 66 mm. long, the longest females 80 to 114 mm. The longest female in each of these four series is 1.5 to 2.0 times as long as the longest male. The longest females would be about 3.5 to 8.0 times as heavy as the longest males, if the usual approximate cube relation holds. The lesser size of the males seems to hold in all other Collections of the species containing adult fish. The very restricted habitats and the thoroughness of collecting rule out the alternative suggestion that the older and larger males were unavailable.

The occasional occurrence of apparently oversized and perhaps overage females (fig. 51), particularly at Collection 17, is discussed under Size (pp. 208–209 and fig. 50).

A comparison of the proportional measurements for the smaller and larger males, and for the smallest, medium, and largest females, by geographical areas (table 36), gives some indication of some sexual differences in changes with growth in the relative size of the body and head parts and of the fins, as follows:

Predorsal length: approximately isometric in males, increasing in females, markedly so in oversized fish (p. 215).

Anal origin to caudal base: increasing in males, except for the dwarf population of Ruby Valley; decreasing in females (presumably by reason of an increase in length of abdomen—a frequent occurrence in females).

Body depth, caudal-peduncle depth, and, contrary to a general trend in fishes, head length: all fluctuate without apparent marked trend.

Orbit length: decreasing in both sexes, as almost always in fishes.

Upper-jaw length: about isometric in males, probably slightly increasing in females.

Mandible: probably decreasing slightly in each sex.

Interorbital width: decreasing slightly in each sex.

Suborbital width: about isometric in males, increasing in females.

Fins: all decreasing in both sexes.

TABLE 40. *Sexual dimorphism in predorsal and fin lengths in* Relictus solitarius, *expressed as excess for males over females in mean values in permillage of standard length.*[1]

Pluvial lake system Valley	Predorsal length A	B	C	Dorsal fin A	B	C	Caudal fin A	B	C	Pectoral fin A	B	C	Pelvic fin A	B	C
Lake Franklin															
Ruby	4	−13	—	17	37	—	0	19	—	35	37	—	21	31	—
Butte	−7	−19	−27	37	34	51	20	13	15	44	45	46	33	13	37
Lake Waring	−4	−17	−28	30	32	46	8	7	30	44	34	45	31	26	34
Lake Steptoe	−10	−13	−18	12[2]	35	44	6[2]	6	23	2[2]	27	34	4[2]	28	34
Lake Spring	−2	−19	−29	32	46	53	7	8	13	45	47	49	30	36	39
Total	−3	−17	−23	25	35	47	10	6	21	36	38	44	24	27	35

[1] Data from tables 36, 37, which indicate number of specimens measured of each size group, two for males and three for females. In column A and B males of the smaller and larger size group are compared, respectively with females of the same size groups; in column C the larger males are compared with the largest size group of females (larger than any males).

[2] Data are aberrant because the fish in the small-size category are only 27–37 mm. long, and had presumably not yet developed much sexual dimorphism in the length of the fins.

Sexual dimorphism in size of all fins is strongly marked in this species. The greater length of the fins in the males (table 40), expressed as excess in males of the mean value in permillage of standard length, is much greater for the dorsal fin than in either *Rhinichthys osculus* (table 14) or *Gila bicolor* (table 28) samples—the excess values are relatively consistent, closely approximating those for the pectoral and pelvic fins. The excess values fluctuate from slight to moderate for the caudal fin, as they do for the two other species. The excess values for the pectoral and pelvic fins are somewhat more consistent than for the other species. In grand average, the pectoral is about 4 percent, the pelvic about 3 percent, of the standard length longer in the male than in the female. Such rather extreme sexual dimorphism may be regarded as an example of exuberance, such as we mentioned for certain races of *Lucania parva* (Hubbs and Miller, 1965, p. 33).

In the males, the fins are not only elongated but are also broadened, and the rays are thickened, especially along the front or outer edge. Thus, the sexes are notably sexually dimorphic.

In several respects, the breeding males tend to develop the adult coloration at a smaller size than the females and carry the development farther. This was noted, for example, in the attainment of dense puncticulation on the upper and lower lips and on the intergular region.

The characteristics of the nuptial tubercles, as briefly indicated in the generic diagnosis (p. 182), furnish some of the more distinctive features of the relict dace. The following description was drawn from males in Collections 17 and 25, but at least incipient development of the same type was noted for several other Collections, and it is assumed that the pattern is species-specific. On the head, the largest of the distinctively straight, cone-shaped tubercles line the infraorbital branch of the lateral line uniserially. The next most prominent tubercles line the suborbital margin, also uniserially. In addition, very small cones are scattered over the lower-cheek and mandibular regions, and, in some males, a few develop just behind and above the eye.

On the pectoral fin rather large but definitely caducous and very distinctive erect cones extend uniserially along the upper edge of the topmost (outermost) ray, curving to an inner position on the ray posteriorly (in *Rhinichthys osculus*, the much thickened uppermost ray is devoid of tubercles; in *Gila bicolor*, small, firmly attached, curved tubercles line the first ray uniserially). In addition, similar but usually smaller organs extend along the next one to four rays, leaving the

TABLE 41. *Number of fin rays in certain Collections of* Relictus solitarius *in different drainage basins.*

Pluvial lake system / Valley (Coll. no.)	Dorsal Rays[1]						Anal Rays[1]				
	7	8	9	10	No.	Mean	6	7	8	No.	Mean
Lake Franklin											
Ruby (1, 3, 5, 6)	4	26	—	1	31	7.93	1	30	—	31	6.93
Butte (7)	2	18	—	—	20	7.90	1	19	—	20	6.95
Butte (11)	—	15	—	—	15	8.00	3	12	—	15	6.80
Lake Waring (17)	—	20	—	—	20	8.00	—	20	—	20	7.00
Lake Steptoe (26, 27)	1	24	1	—	26	8.00	1	23	2	26	7.04
Lake Spring (32)	1	19	—	—	20	7.95	1	19	—	20	6.95
Total	8	122	1	1	132	7.96	7	123	2	132	6.96

Pluvial lake system / Valley (Coll. no.)	Caudal Rays[2]								Pelvic Rays[3]						
	16	17	18	19	20	21	No.	Mean	5	6	7	8	9	No.	Mean
Lake Franklin															
Ruby (2)	1	—	—	20	—	—	21	18.86	—	—	7	39	4	50	7.94
Butte (7)	—	—	1	14	2	1	18	19.17	—	—	4	34	2	40	7.95
Butte (11)	—	—	1	12	—	—	13	18.92	—	—	1	28	1	30	8.00
Lake Waring (17)	—	1	3	13	3	—	20	18.90	—	—	—	29	11	40	8.27
Lake Steptoe (26)	—	—	1	14	2	1	18	19.17	—	—	4	30	6	40	8.05
Lake Steptoe (22)	—	—	—	—	—	—	—	—	1	2	28	177	20	228	7.93
Lake Spring (32)	—	2	2	9	1	—	14	18.64	—	—	5	32	3	40	7.95
Total	1	3	8	82	8	2	104	18.95	1	2	49	369	47	468	7.98

Pluvial lake system / Valley (Coll. no.)	Pectoral Rays									
	9	10	11	12	13	14	15	16	No.	Mean
Lake Franklin										
Ruby (2)	—	—	—	1	14	17	5	3	40	13.87
Butte (7)	—	—	—	—	8	22	5	5	40	14.17
Butte (11)	—	—	—	2	10	9	7	2	30	13.90
Lake Waring (17)	—	—	—	3	16	20	1	—	40	13.48
Lake Steptoe (26)	1	—	—	2	9	12	15	1	40	13.97
Lake Spring (32)	—	—	—	4	16	10	4	6	40	13.80
Total	1	—	—	12	73	90	37	17	230	13.87

[1] Last 2 elements counted as 1 ray.
[2] Principal rays (branched rays +2)
[3] Both sides counted

proximal and distal parts of the rays unarmed. The files remain uniserial throughout the ray, not branching, as they diagnostically do in *Rhinichthys* and *Gila*. In high males, similar but weaker tubercles occur along each of the outer one to several pelvic rays and along each of the anteriormost one to a few anal rays. No nuptial tubercles ever develop on the body.

In nuptial males the fin rays are considerably thickened, especially along the anterior (or upper or outer) edge of the fin.

FIN RAYS (table 41). As in *Rhinichthys* and *Gila bicolor*, the dorsal rays rather seldom vary from 8; when they do, the number is more often 7 than 9 or 10. As in *Rhinichthys osculus*, the anal rays (6–8) seldom deviate from 7; the usual number in *Gila bicolor* is either 7 or 8. The caudal rays vary widely, from 16 to 21, about as in the *Rhinichthys osculus* and *Gila bicolor* samples, but in this species the deviates from the family norm of 19 are about as frequently up as down. The pectoral rays vary in number from 12 to 16, with a single count of 9, and with a grand-total mean of 13.87, lower than for any of the samples of *Gila bicolor* treated; about equal to most means for the samples of *Rhinichthys osculus robustus*,

TABLE 42. *Number of vertebrae in certain Collections of* Relictus solitarius *in different drainage basins.*

Pluvial lake system Valley (Coll. no.)	Frequencies[1] 35	36	37	38	39	No.	Mean
Lake Franklin							
Ruby (2)	—	5	6	1	1	13	36.85
Butte (7)	2	14	3	—	—	19	36.05
Butte (11)	1	2	4	5	—	12	37.08
Lake Gale							
Butte (13)	—	4	8	1	—	13	36.77
Butte (14)	—	3	6	1	—	10	36.80
Lake Waring							
Goshute (16)	—	8	6	—	—	14	36.43
Goshute (17)	2	7	2	1	—	12	36.17
Lake Steptoe							
Steptoe (22)	1	6	8	—	—	15	36.47
Steptoe (25)	1	9	4	1	—	15	36.33
Lake Spring							
Spring (33)	—	10	4	2	—	16	36.50
Total	7	68	51	12	1	139	36.51

[1] Including hypural complex as 1 vertebra and including the four comprising the Weberian apparatus.

but higher than the means for the isolated subspecies. The pelvic rays range from 7 to 9 and usually number 8, as in the isolated spring populations treated of *Gila bicolor* (modally 9 in *G. b. obesa*) and as in the Humboldt Valley populations of *Rhinichthys osculus robustus* (usually reduced to 7 in isolated spring samples of *R. osculus*). In summary, the ray numbers show some evidence toward reduction in this spring-inhabiting fish. No marked regional variation is noted. Ray counts in the holotype are D 7, A 6, P_1 14—15, P_2 8—8, C 19.

VERTEBRAE. The vertebrae (table 42) number 35–39, usually 36 (36 in holotype) and/or 37 (37 or 38 in one Collection), much as in the forms of *Rhinichthys osculus* treated (35–40, usually 36–39), somewhat less than in the subspecies of *Gila bicolor* handled (37–42, usually 38–40). Of the ten representative Collections counted, only one of two from the section of Butte Valley that drained directly into Lake Franklin shows a noteworthy divergence from the others.

SCALE ROWS. Numbers of scales in the five rows counted (table 43) usually run somewhat higher than in the forms studied of *Rhinichthys osculus*, but lower than in those of *Gila bicolor*. There is considerable local variation, but overlaps in counts are generally wide and some of the counts are not very precise for reasons cited (p. 91). In general, counts for the drainage basin of pluvial Lake Franklin, especially those for the apparently dwarf form of Ruby Valley, tend to run lower than those for the basin of Lake Waring, but the differences are not sharp enough to warrant subspecific separation. The circumstance that the sample from Spring Valley agrees in scale count best with the samples from the Butte Valley section of the ancient drainage basin of Lake Franklin, is cited as an indication that the source of the assumed introduction into Spring Valley was one of the springs of Butte Valley (p. 235). In the holotype, the scale row counts (all approximate, by reason of irregularities) are: in lateral line, 60; above lateral line, 13; below lateral line (to anal origin), 12; lateral line to pelvic insertion, 9; predorsal, 35; around body, 26 above, 31 below, 59 total.

GILL-RAKERS. The rakers (table 45) vary from 7 to 12 and usually number 8 to 11. With some overlap, they are more numerous than in *Rhinichthys osculus*, but fewer than in *Gila bicolor*. They are also larger and better developed than in *R. osculus*, but smaller and weaker than in *G. bicolor*. The counts average slightly lower for the Butte Valley section of the drainage basin of Lake Franklin and for Spring Valley than for other parts of the range, as do the scale counts, further suggesting that the Spring Valley population may have been introduced from Butte Valley.

PHARYNGEAL ARCH AND TEETH. These structures are discussed above under the heading of the genus. The data (table 33) do not suggest any regional differentiation in tooth number.

KARYOTYPE. Treated under the genus heading (p. 193).

SEXUAL DIFFERENCES IN NUMBERS AND BIOMASS. Among the five large and representative Collections for which data on population structure were accumulated (tables 38, 39), the sex ratio

TABLE 43. *Number of scale rows and sensory pores in certain Collections of* Relictus solitarius *in different drainage basins.*

Pluvial lake system / Valley	Coll. (No.)[1]	Number of scales in each row[2]: Lateral-line rows	Predorsal rows	D-A origins	Around body	Around peduncle	Number of pores[3]: Lateral line	Supra-temporal
Lake Franklin								
Ruby	2 (5)	51–60 55.2	32–34 32.6	20–23 21.6	52–60 54.8	28–30 29.2	3–17 11.8	2–4 3.2
Butte	7 (5)	50–57 54.6	30–33 31.4	21–23 22.4	55–58 55.8	30–31 30.2	13–26 18.4	2–4 3.0
	11 (10)	51–65 58.5	27–36 32.5	21–26 23.3	55–64 60.2	28–30 29.6	6–21 12.9	2–5 3.4
Lake Gale	14 (10)	54–65 60.4	32–36 34.3	22–24 22.8	54–64 58.0	30–32 30.8	11–29 17.9	3–5 3.2
Lake Waring	16 (10)	57–66 62.2	— —	— —	— —	— —	— —	— —
	17 (5)	58–66[4] 60.3	31–39 33.4	22–26 24.8	60–66 62.6	30–34 32.0	11–26 16.7	0–5 3.0
Lake Steptoe	25 (10)	55–66 60.8	— —	— —	— —	— —	— —	— —
	26 (5)	58–70 61.8	30–36 32.8	25–28 26.2	59–61 59.8	32–34 33.0	3–25 17.0	3–4 3.4
Lake Spring	32 (5)	50–55 52.6	30–33 31.2	21–25 22.4	55–61 58.6	29–32 30.4	14–25 18.2	2–4 3.1
Total	— —	50–70 59.1	27–39 32.8	20–28 23.3	52–66 58.7	28–34 30.6	3–29 16.0	2–5 3.2

[1] Collection number, and, in parentheses, number of specimens, except as indicated by footnote.
[2] For each row, the minimum and maximum counts, and the means.
[3] Both pore counts were made on both sides, doubling the number of counts.
[4] 15 specimens.

varied tremendously and unaccountably: from 37 to 173 males per 100 females for the immature fish and from 29 to 99 for the mature fish. In view of the greatly restricted habitats and the thorough collecting, it seems improbable that differential schooling or different habitat directly caused the variation. Differential mortality or some chromosomal aberration would seem to provide a more plausible explanation. Rather small samples may have resulted in some of the fluctuation for the immature fish, but the samples seem adequate for the mature specimens. Oddly, in-

TABLE 44. *Counts of mandibular pores in populations of* Relictus solitarius *in certain basins in Nevada.*

Pluvial lake system / Valley (Coll. no.)	Mandibular Pores: 3	4	5	6	7	8	No.	Mean
Lake Franklin								
Ruby (2)	—	5	24	9	1	1	40	5.23
Butte (7)	—	4	21	13	2	—	40	5.33
Lake Waring (17)	—	4	15	12	6	1	38	5.61
Lake Steptoe (26)	1	6	28	5	—	—	40	4.93
Total	1	19	88	39	9	2	158	5.27

TABLE 45. *Number of gill-rakers in certain Collections of* Relictus solitarius *in different drainage basins.*

Pluvial lake system / Valley (Coll. no.)	Gill-rakers: 7	8	9	10	11	12	No.	Mean
Lake Franklin								
Ruby (2)	—	—	7	12	1	—	20	9.70
Butte (7)	1	4	12	2	1	—	20	8.90
Butte (11)	—	1	11	3	—	—	15	9.13
Lake Waring (17)	—	5	6	7	2	—	20	9.30
Lake Steptoe (26)	—	—	4	9	6	1	20	10.20
Lake Spring (32)	—	7	10	3	—	—	20	8.80
Total	1	17	50	36	10	1	115	9.35

deed, Collection 17 with the lowest proportion (37) of males among the immature fish (unfortunately a small sample) shows a balanced representation of sexes among the adults; whereas Collection 25, with 1.7 males to 1.0 females among the immature fish, had the most unbalanced sex ratio among the adults (3.4 females to 1.0 males).

In as much as the females average larger than the males, and ordinarily outnumber them, the contrast in the total biomass of the sexes must be large.

ABUNDANCE AND LIFE HISTORY. Numerous field observations and local testimony indicate that *Relictus solitarius* is a very prolific fish, with a rather long breeding season, extending at least from late June to mid September (the entire period of collecting). The spawning period is roughly approximated by the frequent collection or observation of the very young at various dates, as indicated by the minimum size reported above in the account of the Collections (pp. 199–207). For example, extremely small fish seen at Collection 4 on September 13 suggested that spawning was still in progress. Inclusion of nuptial males and of gravid females at various times in a number of Collections confirmed the postulate of an extended spawning period.

The prolonged spawning may be related to the moderately warm and presumably relatively constant temperatures of the type of spring waters inhabited by this species (see below).

Great abundance was shown by the very large numbers collected—at times in single hauls of a small seine (as is also indicated in the descriptions of the Collections). Former swarming where the dace have become depleted or extirpated by agriculture, fish-stocking, and industry is indicated in the section on Material Examined and Population Status: in the general remarks on Populations of Ruby Valley; following the account of Collections 10 and 19; in the discussion (pp. 204–207) of Populations of Steptoe Valley, especially in the local testimony (p. 205) "that wagon loads could be gathered when the holes went dry in summer."

That the relict dace deposits its eggs on plants is suggested by its close association with submerged vegetation growing on soft, more or less anaerobic bottom, in regions where any substrate other than the plants is unsuitable.

The size-frequency distribution at representative Collections (table 38), confirmed by inspection of other series, indicates, with the dates of collection in mind, that both sexes spawn first as yearlings, but that the smallest yearlings tend to reproduce late in the second year of life. The rather compact size distribution of the mature males suggests that few males breed at an older age. That the females grow so much larger than the males is an indication that many of them breed when two or more years old. No attempt was undertaken to determine age by a study of annuli on scales, otoliths, or bones.

HABITS. The relict dace is typically a midwater swimmer, in agreement with its body form (p. 212). It is seldom seen either at the very surface or resting on the bottom.

It is one of the most secretive of minnows—more so, we think, than any other western species. On even slight disturbance it tends to dive promptly into the soft bottom or into the thick patches of *Chara* or other submerged plants (usual features of its habitat; see below). Once there, it may remain out of sight for a considerable period. These habits were particularly striking when first observed on September 12, 1934, evoking a field note, for the springs and open marshes of Ruby Lake. Here, the secretiveness may have been accentuated as an escape behavior, in the pressure from the abundant waterfowl.

That the relict dace may become especially retiring during cold periods is suggested by observations on September 13–14, 1934, when water froze in our camp overnight. No minnows were seined or seen on a careful observation of the spring-fed waters from about 2 km. south of Currie to the source, in a pond about one-half acre in size, or in two tributary groups of mound springs just to the west. The pond at the base of lava hills had the typical features of *Relictus* habitats: heavy growth of *Chara* and *Nasturtium*,

algae, *Potamogeton*, cf. *P. pectinatus*, cane, etc., with open spaces. That the species eluded observation during that cold period is indicated by our later seining of 201 specimens in these waters (Collection 19), and by local testimony on their presence (p. 219).

The relict dace seems to be a hardy fish. A rancher who has used it said that it serves well as live bait in sport fishing and that it lives long when thrown out on the bank. None died during transport by car to Michigan.

Habitat. Our field exploration confirmed the local testimony that this minnow occurs throughout Butte Valley, "without variation," in all "warm" springs (obviously meaning those that are not hot, nor definitely cold, and do not freeze in the winter). We found this to be generally true throughout the range of the species. It seems to be absent in all canyon streams. When the species was common in spring waters in Ruby Valley, in 1934, we found none in Cave Creek, an icy-cold stream that discharged from a large cave (mentioned by Wheeler, 1889, p. 26), nor in very cold springs issuing from the same limestone formation nearby—though these waters are in contact with those in which the relict dace flourished.

In the spring-fed waters where it occurs, it tends to concentrate in quiet pools, particularly those that are well vegetated, and where the banks are undercut.

The temperature of the water was noted at the time of collecting, generally in the hot season, as "cool" or "moderate," or, when measured (in Fahrenheit scale, transposed to nearest Celsius degree), as 9°, 12°, and 14° (once each); 15° and 16° (twice each); 18° (four times); 19° and 20° (once each), 21° (four times), and 22°, 23°, 24°, and 25° (once each).

The vegetation was recorded as "little" only thrice; "some" or "moderate" (twice); "much," "dense," "generally dense," or "rather thick" (13 times), and "choked" or "generally choked" (5 times). The plants were identified roughly as *Nasturtium* (water cress), *Potamogeton*, cf. *P. pectinatus*, broad-leaved species of *Potamogeton*, *Chara*, *Utricularia*, rush, bur-reed, grass, alga, and moss.

As noted under Habits, above, the relict dace on even slight disturbance dives into the thick vegetation, and remains hidden for a considerable time.

Utilization. The ranch operator at Stratton Ranch in Butte Valley testified on June 2, 1942, that he had taken this minnow from there to Lake Mead, where they served satisfactorily as live bait for gamefish. It was further stated that it has been used as "scent" in trapping coyotes. Ranchers said also that it has been eaten, "as sardines."

Another possible utilization of the relict dace came to our attention on June 6, 1942, when the owner of Morgan Ranch Spring in Rush Valley, Tooele County, Utah, who was developing a resort there, told us that in building up a stock of bullfrogs he had utilized a fish that we assume to be this species. He had heard that minnows serve as food for bullfrogs and that minnows are common at the McGill Ranch in Steptoe Valley, so he went there, three years previously, and brought over three barrels of "small blue minnows," avoiding the "goldfish." These were almost certainly representatives of *Relictus solitarius* (see Collection 25, p. 205). However, hundreds of Utah chubs (*Gila atraria*), either native or also introduced, were the only fish we saw in his spring, and it appeared doubtful that any relict dace had survived. The water temperature, about 29.5° C., may well have been too hot for *Relictus* (see above).

The introduction of the relict dace into Spring Valley, presumably at Stone House (pp. 233–235) may have been for mosquito control, or perhaps as a curiosity.

Derivation of name. The Latin term *solitarius* is defined as "alone, by itself, lonely, solitary." It refers to the evidence that *Relictus solitarius* is the lone native inhabitant of any of the four Pleistocene lake basins in which it naturally occurs.

GENUS CRENICHTHYS HUBBS

Crenichthys Hubbs, 1932, pp. 1–4, fig. 1 (diagnosis; comparisons and relationships; type, *C. nevadae*). Brues, 1932, p. 280 (distinct genus; relationships). Sumner and Sargent, 1940, pp. 46–54 (*C. baileyi* recognized by Hubbs; physiology and hot-spring habitat). Hubbs, 1941a, p. 66 (mention of discovery). Hubbs and Miller, 1941, p. 1 (distribution; *C. baileyi* included in genus). Sumner and Lanham, 1942, pp. 313–327, figs. 1–4 (physiology and hot-spring habitat). Hubbs and Miller, 1948b, pp. 90–91, fig. 24 (distribution; species). Miller, 1948, pp. 99–100 (relationships; distribution). Kopec, 1949, pp. 56–61 (history of genus and species; biology of *C. baileyi*). La Rivers, 1952, p. 90 (characters in key; compared with *Empetrichthys*; "Springfish"). Eddy, 1957, p. 162 (characters in key; desert streams). Moore, 1957, pp. 150–151 (comparisons, in key; teeth; species; range). Miller, 1958, pp. 206–207, figs. 15, 16 (two species; distribution as isolated relict). Hubbs and Drewry, 1962, pp. 107–110 (artificial hybridization regarding relationships). La Rivers, 1962, pp. 21, 31, 87, 109, 512–516, 681–686 (range; environment; conservation; review of literature). Uyeno and Miller, 1962, pp. 520–532, figs. 2B, 3B, 5B, 7 (relationships; osteology and dentition; distribution). Bradley and Deacon, 1965, pp. 55 and App. II, p. 2 (habitat and community of both species). Hubbs and Hettler, 1965, pp. 245–248 (tolerance to environment). Hubbs, Baird, and Gerald, 1967, pp. 104–115, figs. 1–3 (activity cycles related to diurnal fluctuations in dissolved oxygen). Moore, 1968, pp. 109–110 (comparisons, in key; diagnosis; species). Hubbs, 1970, pp. 295–296 (artificial hybridization regarding relationships).

Additional papers bearing on the responses of *Crenichthys* to its environment, and on the threat to this native genus resulting from the introduction of exotic fishes, but dealing with *Crenichthys baileyi*, are: Deacon, Hubbs and Zahuranec, 1964; Hubbs and Deacon, 1965; Wilson, Deacon, and Bradley, 1966; Deacon and Wilson, 1966 and 1967; Cole, 1968, p. 477; Minckley and Deacon, 1968.

We have already referred to this cyprinodont genus as one of the two types of fish that inhabit the warm springs of Railroad Valley, in which pluvial Lake Railroad accumulated, and the long chain of warm springs in the remnant course of pluvial White River (p. 35), just to the east. In addition, we have referred to it, further (p. 71), as one of the inhabitants of the north-central Great Basin.

We have verified the specific distinctness of the two forms of *Crenichthys*: *C. nevadae* of Railroad Valley and *C. baileyi* of the White River remnants.

The status and relationships of the relict cyprinodontid genera *Crenichthys* and *Empetrichthys* of the Great Basin have been discussed over the past 40 years, with reference to earlier suppositions, by Hubbs (1932, pp. 1–4), Hubbs and Miller (1941, pp. 1–2), Miller (1948, pp. 99–100), Uyeno and Miller (1962), and Hubbs and Drewry (1962). On the basis of hybridizing potential, Hubbs (1970, pp. 293–296) suggested that *Crenichthys* and the alien, western species of *Fundulus*, *F. parvipinnis* Girard, are closely related. This view indeed seems to make sense, in view of the zoogeographical and paleontological data. Without entering here into a renewed study of *Crenichthys* and its relationships, we have merely brought together the preceding annotated synonymy of the genus.

Railroad Valley Springfish

Crenichthys nevadae Hubbs.

Crenichthys nevadae. Hubbs, 1932, pp. 1–6, pl. 1 (original description of genus and species; isolated warm spring at Duckwater, Nye County, Nevada). Brues, 1932, p. 280 (type habitat). Sumner and Sargent, 1940, p. 46 (mention). Hubbs, 1941a, pp. 66–67, fig. 5(collection of types; abundance in hot springs of Railroad Valley). Hubbs and Miller, 1941, pp. 1–2 (type of *Crenichthys*; in hot springs of Railroad Valley, replacing *C. baileyi*; compared with *C. baileyi*); 1948b, pp. 90–91, 93, fig. 24 (hot springs in Railroad and Duckwater valleys). Kopec, 1949, p. 56 (discovery of species). La Rivers, 1952, p. 91 (characters in key; compared with *C. baileyi*; Railroad Valley system, west of White River; "Railroad Valley Springfish"). La Rivers and Trelease, 1952, p. 118 ("Railroad Valley Springfish"; counterpart of *C. baileyi*). Eddy, 1957, p. 162, fig. 406 (coloration; Railroad Valley; "Railroad Valley springfish"). Moore, 1957, pp. 150–151, fig. 2-82 (color; teeth; Railroad Valley; "Railroad Valley springfish"). Frantz, 1958, p. 7 (in lake and steam survey, *fide* La Rivers, 1962, p. 517). Miller, 1958, p. 206, figs.

15, 16 (relict habitat). BAILEY *et al.*, 1960, p. 21 (freshwater; "Railroad Valley killifish"). LA RIVERS, 1962, pp. 27, 512, 517–520, figs. 231, 232 ("Railroad Valley springfish"; scientific-name and vernacular synonymies; original description quoted in full; type locality; range; transplantation to near Sodaville, Nevada; taxonomy; compared with *C. baileyi*; physical data on habitat; associated fauna; newly hatched young in December). UYENO and MILLER, 1962, p. 522 (material studied). BRADLEY and DEACON, 1965, App. II, p. 2 (abundant, Railroad Valley). HUBBS and HETTLER, 1965, pp. 245–248 (physical habitat; tolerance). HUBBS, BAIRD, and GERALD, 1967, pp. 104–115 (activity cycles related to diurnal fluctuations in dissolved oxygen; sound production; Duckwater Spring and Lockes Ranch Spring, Nevada). COLE, 1968, p. 477 (environmental factors, both species). MOORE, 1968, p. 109 (compared with *C. baileyi*; Railroad Valley; "Railroad Valley springfish"). BAILEY *et al.*, 1970, p. 30 (freshwater; "Railroad Valley killifish").

As noted before (p. 71), the detailed systematic treatment of *Crenichthys* and of *C. nevadae* is deferred.

It seems virtually certain that *Crenichthys nevadae* has maintained existence, as native, only in the warm springs of Duckwater Valley, a floodwater arm of Railroad Valley, and in the warm springs on Lockes Ranch in the northwestern part of the main valley, both in Nye County, Nevada. Following are data on preserved specimens of the species in the Museum of Comparative Zoology, Harvard University; University of Michigan Museum of Zoology; United States National Museum; University of Nevada, Las Vegas; Nevada State Museum; and Arizona State University.

- MCZ 32948 (holotype), and UMMZ 95024 (paratype): isolated warm spring at Duckwater, near north end of Warm Spring Valley, 16 miles south and 46 miles west of Ely (originally misstated as 16 miles east and 46 miles south of Ely—see La Rivers, 1962, p. 518), in T. 12 N., R. 56 E.; caught in a glass jar by Dr. and Mrs. C. T. Brues on July 21, 1930, from the then abundant population; the holotype and the paratype are maturing females respectively 44 and 29 mm. in standard length.
- UMMZ 124941 and USNM 117509: Warm Spring pool at source of Duckwater Creek, 5.2 miles by road above Duckwater, in T. 13 N., R. 56 E.; seined by Carl L. Hubbs and family on August 18, 1938, from the then teeming population; 778 young to adult, of both sexes, 10–55 mm. long.
- UMMZ 132176: spring and outlet, tributary to Duckwater Creek, beside Indian Colony, in T. 12 N., R. 56 E.; seined by Carl L. Hubbs and family on September 9, 1934, from a teeming population; 1,677 young to adult, 13–71 mm. long.
- UMMZ 132178: Duckwater Creek about 3 miles above Duckwater Store, in T. 12 N., about on R. 55–56 line; seined by Carl L. Hubbs and family on September 8, 1934; 23 young to adult, 18–39 mm. long.
- UNLV 119: spring near highway at Duckwater; J. E. Deacon, Karl Larsen, and Ken Giles; August 31, 1961; 166, 6–42 mm. long.
- UNLV 520 and ASU 3904: Duckwater; J. E. Deacon; June 5, 1964; 106, 19–54 mm. long.
- UNLV 552 and ASU 4124: Duckwater; J. E. Deacon and M. B. Rheuben; September 15, 1964; 64, 13–34 mm. long.
- UNLV 946 and ASU 4218: Duckwater Spring; J. E. Deacon; October 2, 1966; 18, 27–51 mm. long.
- UMMZ 132173 and Nevada State Museum: large hot spring on Lockes Ranch in Railroad Valley, about a half mile from the ranch house, in T. 8 N., R. 56 E.; taken by derris by Carl L. Hubbs and family on September 8, 1934, as a small portion of the teeming population; 1,158 young to adult of both sexes, 10–55 mm. long.
- UMMZ 132175: two other pools on Lockes Ranch; taken by Carl L. Hubbs and family on same day, by hand and small seine; 65 young to adult, 18–41 mm. long.
- UMMZ 181745: main hot spring on Lockes Ranch, ca. a half mile northeast of main ranch house; seined by Robert Rush Miller and family on July 16, 1963; 319 young to adult 15–49 mm. long.
- UNLV 261: ditch at Lockes Ranch; J. E. Deacon, Clark Hubbs, and Bernard J. Zahuranec; February 2, 1963; 29, 9–28 mm. long.
- UNLV 609 and ASU 3905: Lockes Ranch; J. E. Deacon; June 5, 1964; 112, 14–51 mm. long.
- UNLV 905: Lockes Ranch Spring; J. E. Deacon; October 2, 1966; 271, 11–40 mm. long.

No evidence was found in our field work of 1938 that *Crenichthys* lives in the various cool springs, on the east side of Railroad Valley, in which local forms of *Gila bicolor* occur (Hubbs and Miller, 1948b, p. 91). Nor have we found it, either then or in 1969, in Currant Creek, the eastern tributary to the valley, either in the lower

section, near the Currant Store, or higher in the creek.

Fortunately for its perpetuation, since the species is so limited in habitat and distribution, *Crenichthys nevadae* has been successfully transferred outside the study area. The intentional transplant was thus recorded by La Rivers (1962, p. 518):

> . . . . Successfully transplanted by Tom [Thomas J.] Trelease into artificial ponds at Sodaville, southeastern Mineral County on September 4, 1947. This natural seep of warm water on the west side of U. S. Highway 95 was later enlarged by bulldozer action into a small pond. The transplant was motivated because of the possibility that blackbass would be planted in the springfish's home locality. The 6 original fish have become many.

Having heard in 1970 of the abundance of a small fish seemingly of this type about Sodaville, Miller and family checked the report on July 2, 1970, and indeed found *Crenichthys nevadae* still abundant in the hot springs (36–38° C.; air 34°), particularly in the lower of the two shallow pools that have been dug out. The pool at the head spring measured ca. 4 × 6 m. and the lower one ca. 6 × 6 m. Two more, quite small springs, with some springfish, open between the two pools, and the total outflow feeds into an elongate, deeper pond, with much vegetation, in which no fish could be seen. In the two pools containing the springfish the water was clear but very easily roiled: the bottom was of flocculent silt and hardpan, with some gravel; the vegetation comprised green algae and, marginally, *Scirpus* and *Juncus*. The springs are across the highway from Sodaville (American Mining Corporation).

TRANSFERS OF GREAT BASIN FISHES (OTHER THAN GAME SPECIES) INTO, BETWEEN, AND FROM THE NORTH-CENTRAL BASINS

Before considering the introductions of more exotic fishes into the north-central Great Basin, to enhance the sport fishery and for other purposes, we treat the highly probable to certain transferences by man of fish species endemic to the Great Basin into, between, and out of some of the 21 endorheic basins under study. We have found evidence for fifteen such transfers, involving ten Great Basin fishes. The Utah chub, *Gila atraria*, has been introduced once, we suppose, into each of four among the 21 basins. *Catostomus (Pantosteus) platyrhynchus, Rhinichthys osculus robustus, Gila robusta jordani, Richardsonius egregius, Moapa coriacea*, and *Empetrichthys latos latos*, all exotic to the 21 basins, have each been stocked once into a single basin. The same subspecies of *Rhinichthys* and the species *Relictus solitarius* have each been transported once from one of the north-central Great Basin endorheic units into another. *Gila bicolor* subspecies almost surely, *Relictus solitarius* probably, and *Crenichthys nevadae* certainly, have each been transferred into a basin outside the study area. Particulars are given or referenced below, under species headings.

Because anomalous distributions have generally gone undocumented, and because they may be of considerable potential zoogeographical confusion, much effort has been expended, through extensive local inquiry, through examination of old maps, and otherwise, to arrive at a definite or highly probable conclusion as to whether each anomaly is attributable to a natural or an artificial event. Some of our conclusions rest on differential plausibility, and some reverse our former evaluation, for instance in regard to the native or introduced status of *Catostomus* and *Relictus* in Spring Valley.

Catostomus (Pantosteus) platyrhynchus (Cope).

Through a reappraisal of the evidence, we now attribute the occurrence of a mountain sucker (*Pantosteus*) in Spring Valley, the site of pluvial Lake Spring, to an introduction, rather than to the survival of a Glacial relict. In our early summary (Hubbs and Miller, 1948b, pp. 56–57) we mentioned having heard that small fish occur in

"minor springs forming a series on the east side of the valley," and we reported our collection of two species in Spring Creek, the northern axial tributary to the enclosed Spring basin. The report of fish on the east side of the valley referred, we now think almost certainly, to the introduced Utah chub, *Gila atraria*, far to the south. One of the species collected in Spring Creek was *Relictus solitarius*, for which we find evidence (pp. 233–235) that it was introduced into the basin. The other species was the mountain sucker, which we characterized as "a rare one, ... a new sucker, with characters that line it up best with a Bonneville, or possibly a Colorado species." Still thinking the species to be distinct, one of us (Miller, 1952, pp. 14, 28–29, fig. 13), after examining a few similar specimens of doubtful provenance being sold in southern Nevada for bait, called it the "dusky mountain-sucker, *Pantosteus* species" and stated that it is known only from the northern part of Spring Valley. It was so rare there in 1938 that we could collect by prolonged effort only three specimens, along with 1,073 of *Relictus*; after the first sucker was taken, two hours of further seining yielded only two more. This was at Collection 32 (p. 207) for *Relictus*, in a short, spring-fed section of Spring Creek, at the historical old Stone House. In a strenuous effort to obtain more specimens just 21 years later, at the same place, we took 498 relict dace, but not a single sucker. Furthermore, Collections 30 and 31 in springs issuing in the same stream bed, taken in 1964, comprised 80 and 99 specimens of *Relictus* but not one sucker. Nor has any other trace of suckers been found in Spring Valley (or in any of the other basins here treated).

The location of the Stone House on the old Overland Mail Route, later the Lincoln Highway, presumably facilitated a transfer of the sucker from some place in either the Bonneville or Lahontan watershed. The sucker as well as the dace may well have been brought in for bait or forage, for the flow was more ample when the senior author crossed this stream at the same place in the summer of 1915, on the return from participating in John O. Snyder's survey of the Bonneville fish fauna.

Smith (1966, pp. 58–72, fig. 13) synonymized *Pantosteus* as a subgenus with *Catostomus*, and synonymized the species previously recognized from the Lahontan system, '*lahontan*,' with the one, '*platyrhynchus*,' of the Bonneville system (perhaps under-stressing considerable differences; he also synonymized '*delphinus*' of the upper Colorado River system and '*jordani*' of the Great Plains with '*platyrhynchus*'). Thus, it may not be feasible to determine if the mountain suckers were brought in from the west or from the east. Better agreement of the Spring Valley specimens in number of vertebrae with samples from the Humboldt River system than with those from the Sevier River drainage (Smith's fig. 7, pp. 30–31) is a slight indication of introduction from the west. Our recognition of a distinct species for the Spring Valley fish, and the proposed vernacular of "dusky mountain-sucker," were based largely on the intensity and wide spread of the dark color, which may well have been directly induced by the occurrence of the fish, at the time of capture, in extremely dense vegetation.

Rhinichthys osculus robustus (Rutter).

There is documentary evidence (pp. 107–109) that this species was twice introduced into Ruby Lake by the Nevada Fish and Game Commission to serve as forage for the largemouth bass, *Micropterus salmoides*, the object of a local sport-fishery. The first introduction, in 1950, was from a headwater of Humboldt River; the second, in 1951, from "Sadler's Ranch" (*i.e.*, Big Shipley Spring) in Diamond Valley. There is indication of a very local and limited establishment, from the first stocking only. The first transfer was from outside the basin complex here under special treatment; the second, between two of the 21 endorheic units under study.

Richardsonius egregius (Girard).

"Red-striped shiners," obviously of this species, were included with speckled dace in the 1950

transfer, just recounted, from a headwater of Humboldt River into Ruby Lake. Apparently this stocking has not survived, nor has this Lahontan species managed to persist in any of the lake basins under treatment that formerly discharged into Humboldt River.

Gila atraria (Girard).

The Utah chub, which stands in ill repute among fishery biologists because of its tendency toward population explosion and habitat dominance in artificial impoundments, has, we confidently believe, somehow gained entrance from its native waters of the Bonneville system into four of the 21 basins that are included in the present study. These intrusions have been into springs at Shoshone in Spring Valley, in the basin of pluvial Lake Spring (p. 64); into springs at Geyser Ranch in Lake (Duck) Valley, in the basin of Lake Carpenter (p. 66); into springs at Murphy Ranch in Steptoe Valley, in the basin of Lake Steptoe (p. 58); and into Comins Lake, in the basin of Upper Lake Steptoe (p. 60).

The assumption that the stock of Utah chubs found persisting in Spring and Lake valleys resulted from introductions is complicated by the circumstance that these valleys are separated from upper Snake Valley by a low, flat sill, on the east side of which, not far distant, Utah chubs occur, presumably as natives, in Big Springs and the adjacent slough south of Garrison, Utah, in the pluvial drainage basin of Lake Bonneville. It might be theorized than an ancient outlet into the Bonneville system, or some other stream connection, could have led to the penetration of this chub into Spring Valley. However, there is no definitive evidence of such a discharge (p. 63), and no other indication of the occurrence of Bonneville fishes in Spring Valley. Even the trout was almost surely introduced (p. 64). Furthermore, the low passes would have facilitated the short-distance transport of chubs by man into Spring and Lake valleys, particularly during the years of early settlement. Indeed, as has already been briefly noted, by Miller and Alcorn (1946, p. 182), by us (Hubbs and Miller, 1948b, pp. 55, 57, 100), by La Rivers and Trelease (1952, p. 116), and by La Rivers (1962, p. 397), direct testimony has indicated the introduction of the Utah chub into the springs at Shoshone and at Geyser Ranch. On August 22, 1938, John Yelland told the senior author at Ely, Nevada, that this fish was almost certainly introduced by the original Mormon settlers into both sets of springs. This obviously well informed, well preserved, and reliable man came into Steptoe Valley in 1881 and soon moved into Spring Valley. He volunteered that the chubs were stocked from Utah into the springs at Shoshone, where settlers named Swallow came in from Fillmore, Utah, in the 1870's or earlier. The old homstead in T. 11 N., R. 67 E., is still known as Swallow Ranch, and the Yelland Ranch is in T. 16 N., R. 68 E. Mr. Yelland added that the region about Geyser was settled about 1888 by pioneers, from Utah, named Edwards, Redheffer, and Wintergreen.

It is even possible that Indians may have brought Utah chubs into Shoshone Spring. In his "Nevada Place Names" Leigh (1964) stated, under "Shoshone," that the postoffice was given this Indian name when it was established in 1896 for the Swallow Ranch, which was an ancient rancheria "in the head of Spring Valley, southerly from Wheeler Peak."

As noted in the four articles cited above, respectively on pp. 182, 55, 116, and 387, we found another population of *Gila atraria* at Murphy Spring, in Steptoe Valley, where this species appeared to have been recently established, along with other fish, including the predatory *Archoplites*, which, together, seem to have replaced the native relict dace (p. 58). That occurrence, furthermore, seems too isolated to suggest indigenity. It seems plausible that the chubs were brought there for forage.

Unexpectedly, in August, 1969, Miller found *Gila atraria* swarming in Comins Lake, Steptoe Valley, under conditions even more conclusively indicative of introduction (p. 60). On inquiry, Thomas J. Trelease, Chief of Fisheries for the

Nevada Department of Fish and Game, indicated inability to find any record of the stocking of this fish, and thought that its establishment probably resulted from introduction of bait. Or, the chubs may have been stocked to supply forage for the well established gamefish. Local testimony indicated that a Mr. Swallow formerly operated the CCC (now C–B) Ranch nearby, in the bend of Steptoe Creek, and it is to be recalled that an early settler, at Swallow Ranch in Spring Valley, next eastward, was named Swallow, and that the early Mormon inhabitants in that area are thought to have brought in Utah chubs, which we found there in abundance (pp. 64, 231). These circumstances suggest that the introduction may have come from near Shoshone, the site of the old Swallow Ranch.

Gila robusta jordani Tanner.

The Pahranagat chub was stocked on September 26, 1972, in one of the spring-fed refugium ponds recently constructed at Shoshone, on the east side of the southern part of Spring Valley, Nevada, as part of an effort to insure the survival of threatened species and subspecies of desert fishes (James Yoakum and Dale V. Lockard, personal communications, November, 1972). This subspecies was described by Tanner (1950) as *Gila jordani* and has been discussed by La Rivers (1962, pp. 393–395, fig. 188) under the subspecies designation, in agreement with our appraisal. It is confined to certain springs and spring-fed creeks in Pahranagat Valley, in the course of pluvial White River. The transplant comprised 20 young specimens, which had been caught on the same day in the stream course between the outlets of Crystal and Ash springs. Nearly a month later some were still living in the pond.

Gila bicolor Girard, unnamed subspecies.

The most widespread of the several subspecies of *Gila bicolor* inhabiting the basin of pluvial Lake Railroad (pp. 36, 142) has been found to occur also in Stone Cabin Valley (also known as Willow Creek Valley), just to the southwest, across a definite divide. The discovery of chubs here came as a distinct surprise, for this valley had been included by us in what we had treated (Hubbs and Miller, 1948b, pp. 45–51) as the Area of Sterile Basins, totally lacking in native fish. Having heard that a minnow was common there, the Hubbses, and Boyd W. Walker, collected tui chubs at Stone Cabin Ranch, 55 km. east-northeast of Tonopah, in 1946. They occurred there in the spring waters, in extreme abundance in one pothole spring with flocculent bottom, close to the ranch headquarters. The circumstances clearly suggested an introduction. Local testimony then indicated that the chubs, which had been present for several years, had been brought in from Twin Springs, in Hot Creek Valley [only 40 km. due east, and there is a direct road connection]. Later comparison of the profuse material from each place showed that the specimens from Stone Cabin Ranch (H46–52; UMMZ 144450) agree nicely with those from Twin Springs. Testimony of Forest Ranger Crane, in 1938, that no native fish occur in Stone Cabin Valley (p. 19) is consistent with our findings.

Moapa coriacea Hubbs and Miller.

The Moapa dace was stocked in another one of the refugium ponds at Shoshone, on the same day and for the same purpose as *Gila robusta jordani* was transferred (same personal communications). The genus and species were described by Hubbs and Miller (1948a, pp. 1–14, 28, pl. 1, fig. 1) as endemic in the Moapa River, a tributary of Colorado River, in the lower course of pluvial White River. The transplant of this species also comprised 20 individuals, which were half-grown to adult. Some were seen alive in the refugium nearly a month later.

Relictus solitarius Hubbs and Miller.

Two distributional circumstances suggest the possible transference of the relict dace between minor pluvial basins. We interpret the occurrence of the species in the adjacent Franklin-Gale and

Waring-Steptoe pluvial lake systems as having resulted from an ancient stream transfer (p. 43). The finding of the species in Spring Valley, on the contrary, is not plausibly so explainable, as we have noted (1948b, p. 57). We are convinced that the occurrence of this species, as well as of *Catostomus platyrhynchus* and *Gila atraria*, in this valley, is attributable to introduction by man.

One of the reasons why we think the relict dace was introduced into Spring Valley was thus expressed by us (1948b, p. 56): "Most of the creeks and springs in the valley [Spring Valley] seem to be devoid of native fish life, and Cope and Yarrow (1875) marvelled at the lack of fish in this valley (then named Schell Creek Valley)." This was stated, obviously by Cope, in the brief account of "Siboma atraria var. longiceps, Cope" as follows (on p. 668):

> This variety was discovered by Dr. H. C. Yarrow in Snake Creek Valley, Nevada, who remarked that, while very abundant and the only species of this creek, in Schell Creek Valley, not far distant, no fishes whatever are found. The conditions of life being apparently similar in both streams, their difference in this respect was not explained.

In view of the import of this statement on the original native distribution of the relict dace, a search was made of the early explorational reports and the early maps of the Great Basin, covering the third quarter of the last century, to try to fix the locale of Dr. Yarrow's "Schell Creek Valley." This search failed to verify our belief that his observations can be attributed definitely to Spring Valley. In fact, the early reports and maps seem to have placed this valley and its creek variously along the old Overland Mail Route from the southwestern arm of Antelope Valley westward over the Spring Valley Creek section of Spring Valley to the northern part of Steptoe Valley (as we use this term)—a distance of about 35 km.

The least plausibly correct location of "Shell Valley" (listed by McVaugh and Fosberg, 1941, p. 17) is given in the narrative and accompanying map of Captain J. H. Simpson's report on his epochal exploration in 1858–59 to determine a wagon route from Camp Floyd in Utah to Genoa in Carson Valley (now in western Nevada). A critical reading of the narrative places the valley in the very arid southwestern arm of Antelope Valley, and the draftsman showed it imaginatively as a mountain-rimmed depression. The text describes the basin "as a shallow valley, called Shell Valley, on account of it being covered with shale"! In Appendix A of the Simpson report the Mail Station near the present site of Schellburn is designated "Shell Creek, east side of Steptoe Valley, mail station" (this appendix may well have been added subsequent to the field work and initial narrative, for the publication of the report was delayed until 1876).

Confusion is confounded by the map of Nevada, on a scale of 18 miles to the inch, that was included in "the Commissioner of the General Land Office, 1867, Report for the year 1866" (six years prior to Yarrow's trip, presumably on the same Overland Mail Route, and seven years after Simpson's exploration, but ten years before Simpson's report was published). An earlier large-scale map in the 1862 Commissioner's Report also names the valley, but not in a definitely identifiable position. The 1866 map, which was rather poorly reproduced by Wheeler (1971, opp. p. 108), shows the old Overland Mail Route, including "Capt. Simpson's Route" with the Antelope Spring, Spring Valley, Shell Valley, Shell Creek, and Egans Cañon mail stations so well spaced as to make it appear that the "Shell Valley" station was in the valley of the present Spring Valley Creek, probably close to the old Stone House (the site of Collections 32 and 33 for *Relictus solitarius*, here supposedly later introduced), whereas the Shell Creek station was close to the present axial stream bed of Steptoe Valley, approximately at the present location of "Schellburn," which name over the years has been variously spelled by combining Schell- or Shell- with -bourne, -bourn, or -burn, and has been applied to a mail station, a ranch, a pass, and a fort, all in the same immediate vicinity.

Gibbes' map of California and Nevada, of 1873, prepared, after the mining rush was well underway, by a man who participated in the early surveys (p. 8), shows Schellburn, from which Schell Creek is shown flowing west to the "Slough," with "Schell Valley" named from there northward to the "Sink" (Goshute Lake); therefore in the northern part of Steptoe Valley. Clark and Riddell (1920) also placed Schell Creek in the same position, and noted that it rises in a large spring on the pass.

Obviously the name of Schell Creek has been applied over a rather wide area. In fact, "Schell Cr. D[istrict]." is printed on the Rand, McNally map of 1881 (p. 8) above and well to the east as well as to the west of "Schellburn," which is located on a north–south road (as on some other maps).

"Schell Creek Valley" may well have derived its name from the adjacent Schell Creek Mountains or Range, which presumably in turn derived the name from the minor stream known as Schell Creek (perhaps standing for Schellbourne Creek, just as "Cleve Creek" stemmed from Cleveland Creek). Major geographical features in the general area were named for water sources, which in moister regions are relegated to insignificance. Sulphur Spring Range is another notable example, for the long and lofty range overshadows the minor Sulphur Spring (described under Location G6, p. 154).

The vagaries of geographical nomenclature in the Great Basin, specifically in reference to Schell Creek and the Range, were thus expessed by Leigh (1964, pp. 54–55):

> Schell Creek Range is a long prominent range extending from the southern to the northern limits of White Pine County . . . In the north segment of the range is Schellbourne Pass which was named after a small mining camp nearby. This camp, in the Cherry Creek district, was known at one time as Schell Creek [but Cherry Creek lies on the western side of Steptoe Valley, just north of Egan Canyon], and this cropped form, by extension, was applied to the long important Range. Schellbourne is, of course, a proper name. Schell Creek, near the Pass, was a relay station for the mail riders; soldiers were stationed there for protection of mail and travellers, and the place became known as Fort Schellbourne [on at least one modern map shown in the eastern part of the Steptoe Valley flat]. The cropping of the name from Schellbourne to Schell in early times was not sufficient to Americanize, i.e., corrupt it; the name on modern maps has been reduced to Shell. This is an outstanding example of the gradual downgrading of a place name.

There is, to conclude, no apparent way to determine the definite location of the stream in "Schell Creek Valley" in which Yarrow to his surprise found no fish. It may have been the present Spring Valley Creek, or it may have been Steptoe Creek (the "Slough"), in a portion of Steptoe Valley where the stream is intermittent and may not have contained fish. There seem to be no other plausible alternatives. For evidence on the original absence of the relict dace in Spring Valley we need to return to our own field work and to the experience of early settlers that was recounted to us in 1938.

John Yelland, our convincingly reliable informer (p. 237), avowed that no minnows or other fish originally lived in Spring Valley. A specific reason for relying on his evidence is that he knew precisely where minnows occurred (and still occur) in the springs of Steptoe Valley. He said that he had seen every waterhole in Spring Valley from Shoshone Springs on Swallow Ranch (in T. 11 N., R. 67 E.), where he well knew the Utah chub, to Muncy Creek (in T. 20 N., R. 66 E.). (His old Spring Valley homestead, still mapped as Yelland Ranch, is in T. 16 N., R. 68 E.)

Bert Robison, a rancher native to the valley, testified to us on July 6, 1938, when he was middle-aged, that the deep pools and springs in the main part of Spring Valley, most of which dried up during the great drought of 1934, contained only carp (*Cyprinus carpio*), "perch" (presumably *Archoplites interruptus*), rainbow trout (*Salmo gairdnerii*), and "bass" (obviously *Micropterus salmoides*)—all introduced. He

knew of "minnows" (*Relictus solitarius*) then occurring on his ranch (at the old Stone House, where our Collections 32 and 33 were taken), and he, like John Yelland, knew of minnows in other springs in the north-central Great Basin, where we also knew of them. When on one occasion he drained one of the largest of the pools on Cleveland Ranch to eliminate carp prior to stocking trout, he found no minnows. He knew of no native fish in Shoshone, Worthington, or other springs along the base of Wheeler Peak. On the day of our interview we verified Mr. Robison's testimony by failing to see any fish during a careful examination of a number of the deep spring holes and tule-bordered pools in and below the hay meadows on the northern side of the large and well-watered Cleveland Ranch (near the western margin of T. 16 N., R. 67 E.); nor did we obtain any by seining two very deep pools.

The sharply localized known occurrences of *Relictus solitarius* in Spring Valley (pp. 207–208) are inconsistent with its widespread and swarming abundance (except where locally subjected to major disturbance or predation) in the valleys where it seems surely to be native. Spring habitats that are profuse in Spring Valley, particularly but not exclusively along the western side of the northern part of the valley, at the base of towering Schell Creek Range, seem comparable to those abundantly occupied by the species in Butte and Steptoe valleys. Circumstances seem consistent with the hypotheses that the species was transferred from Steptoe or Butte Valley to Spring Creek at historic old Stone House, as noted in the accounts of Collections 30–33, and that the single population found (Collection 34) in a valley spring on the floor of Spring Valley stemmed from the established stock in Spring Creek through a tremendous flood (p. 207). Two bits of evidence favor the view that the stock of *Relictus* came from Butte Valley: (1) the old Overland Mail Route (p. 233) ran from Spring Valley Creek across Steptoe Valley to Egan Canyon along a course that has not yielded collections of *Relictus* (see fig. 14) and Steptoe Creek is, and was, impermanent, whereas the route from Egan Creek to Ruby Valley (see figs. 12 and 14) ran by springs abounding in the relict dace; and (2) the low scale and gill-raker counts for the Spring Valley series agree better with those for Butte Valley than with those from Steptoe and Waring valleys (p. 224; tables 43, 45). We thus conclude that *Relictus solitarius* has been introduced into Spring Valley, probably from Butte Valley.

There is evidence that *Relictus solitarius* was once transferred to a spring in the Bonneville system of Utah (p. 226).

Empetrichthys latos latos Miller.

This, the only surviving subspecies of the Pahrump poolfish, a cyprinodont, was stocked in April, 1972, in one of the spring-fed refugium pools recently constructed at Shoshone, on the east side of the southern part of Spring Valley, Nevada, as part of an effort to insure the survival of threatened species and subspecies of desert fishes (James Yoakum and Dale V. Lockard, personal communications, November, 1972). This subspecies, along with the species, was described by Miller (1948, pp. 103–104, pl. 11), whose account has been quoted by La Rivers (1962, p. 527, fig. 236). It still exists, very precariously, in a single spring (Manse Spring) in Pahrump Valley, Nevada, within the pluvial drainage system of Lake Manly (of Death Valley). The transplant comprised 15 individuals of varying size, from Manse Spring. Some were seen in the pond in October, 1972.

Crenichthys nevadae Hubbs.

The Railroad Valley springfish has been successfully stocked in warm springs in the Lahontan system (p. 229).

INTRODUCTIONS OF EXOTIC FISHES

A considerable number of exotic fish species, in addition to the mountain sucker and the Utah chub discussed above, have become established

in the area of the north-central Great Basin under treatment. They appear to have contributed moderately to the food and recreational resources of the area, but have also played a role, varying from slight to catastrophic, in the depletion and even in the local extirpation of remnant native fish populations (see following section). In general, because they are members of a much more profuse biota, the introduced fishes are endowed with predatory and competitive capabilities far exceeding those of the few native fishes of the Great Basin, and of other western waters. A major compensation is the degree of adaptation the native fishes have attained, through prolonged and rigorous selection, to continued existence in habitats severely afflicted by desiccation and flooding.

The north-central Great Basin has, happily, hardly been affected by the introductions of tropical home-aquarium fishes, such as have plagued some other parts of Nevada (Deacon, Hubbs, and Zahuranec, 1964; Hubbs and Deacon, 1965; Minckley and Deacon, 1968), and other western states. However, other exotic animals have been introduced into the area. One such is the bullfrog, *Rana catesbeiana* Shaw, which has been widely stocked, for food, in the Great Basin area, where it is regarded as a probable predator on native fishes (Miller and Hubbs, 1960, p. 28; La Rivers, 1962, pp. 434, 441, 475, 525). Most of the known establishments of bullfrogs in the Great Basin are southwest of the area under treatment, but one occurrence is near the northeastern corner of the study area, namely in Warm Springs of Independence Valley, the sole habitat of *Rhinichthys osculus lethoporus* and *Gila bicolor isolata*. Fortunately for the native fishes, two other widely spread exotics, namely the crayfish *Procambarus clarkii* (Girard) and the mosquitofish *Gambusia affinis* (Baird and Girard), are known in the Great Basin largely or wholly from waters south of the study area.

The extent and status of the introductions of exotic fishes into Nevada have been investigated and discussed by Miller and Alcorn (1946), La Rivers and Trelease (1952), and La Rivers (1962), and, for more southern parts of the state, by authors quoted above. To round out the account of the fishes of the study area, we add below, in systematic sequence, a few records and remarks, largely by cross references, to pertinent material listed in the text, as follows:

> by page references to listings of exotic fishes in the first part of this memoir, under the descriptions of the basins of the designated pluvial lakes (pages listed below after the heading "Paleohydrography"); and
>
> by serial Location number in the R series for the subspecies of *Rhinichthys osculus* and in the G series for the subspecies of *Gila bicolor*; and by serial Collection numbers for *Relictus solitarius*.

In general, the exotic fishes reported, observed, or collected were mentioned on the field sheets and in the habitat descriptions based thereon. The species is usually stated or obvious, except for "trout." Some additional data and discussions are presented, tending to show that certain basins in the north-central Great Basin area under study have been devoid of certain native fish species, at least during the historic period.

"Trout"

Paleohydrography: pp. 19 (Monitor Valley), 31 (not native in Clover Valley tributaries), 45 (Ruby Valley tributaries), 60 (Comins Lake), 66 (Wilson Creek in Lake Valley), 68 (Illipah Creek in Jakes Valley), 70 (Pine Creek in Pine Valley).

Location: R1 (Grass Valley). Collection: 14 (Butte Valley).

Also in discussion of springs in Murphy Ranch in Steptoe Valley (p. 206).

All evidence that we have encountered, both positive and negative, points to the assumption that all trout that have been found in any of the streams or lakes within any of the endorheic basins herein selected for study are represented by introduced stocks. Any population that by remote chance may have persisted anywhere in the study area would almost certainly have represented one of the various subspecies of *Salmo*

clarkii, and would in high probability have become modified or eliminated by interaction with introduced trout.

Salmo trutta Linnaeus.

Brown trout have been widely spread in Nevada (Miller and Alcorn, 1946, pp. 174–175; La Rivers and Trelease, 1952, p. 114; La Rivers, 1962, pp. 318–323, 643–645). La Rivers listed the species from within our study area in Skull Creek, Grass Valley, Toiyabe Range; in Pine Creek, Monitor Valley, Toquima Range; in Illipah Creek, Jakes Valley, White Pine Range; and in three streams in Steptoe Valley and five streams in Spring Valley.

Salmo clarkii Richardson, subspecies.

Paleohydrography: p. 64 (Spring Valley).

We have already noted (Hubbs and Miller, 1948b, p. 57) that: "As a result of his survey in 1869, Wheeler (1875: 54) remarked on the lack of fish in the mountain streams of the Great Basin, except in the Humboldt Range and to the east of Snake Range." Any trout that existed in the "Humboldt Range," then largely what is now the Ruby Range, were presumably on the west slope, in the Humboldt River system. We have found corroborative evidence in the History of Nevada (edited by Myron Angel, 1881), where it is stated (on p. 649):

> There are only two streams in White Pine County that have fish in them. In 1876 trout were placed in Cleveland [now "Cleve"] Creek, in Spring Valley, and have multiplied rapidly since. Lehman Creek, which flows into Snake Valley and then sinks, also contains trout, and it is supposed [a probably erroneous supposition] that the Mormons, who formerly occupied a portion of the valley [a correct statement], placed them there.

John Yelland indicated to the senior author on August 22, 1938 (see also p. 245), that the trout stocked in Cleve Creek prior to 1881 were presumed to have come directly or indirectly from Trout Creek, in the Bonneville drainage basin in Juab County, Utah; and further claimed, as a result of much observation in early years, that no fish were native in Spring Valley and that the rapidly established population in Cleve Creek served to stock many of the mountain streams of Spring Valley. On this basis, Miller and Alcorn (1946, pp. 175–178) referred the Spring Valley introduced trout to *Salmo clarkii utah* Suckley, but La Rivers and Trelease (1952, p. 114) and La Rivers (1962, pp. 283–284, 298) have stated that the Utah subspecies presumably no longer persists in this valley in pure form, because subspecies identified as *S. c. lewisi* (Girard) and *S. c. henshawi* Gill and Jordan have also been stocked in east-central Nevada. However, a fine collection of cutthroat trout (13 juveniles to adults, UMMZ 165771), taken by Ted C. Frantz on November 5, 1953, in Pine Creek on the east slope of Spring Valley, on the west face of Mount Wheeler, represents a population distinctively characterized by strong and numerous basibranchial teeth (20–34 or more), large dorsal and anal fins, a long head, and a chunky caudal peduncle—quite different from cutthroat trout in eastern and southern Utah, *Salmo clarkii utah*, and from the Lahontan cutthroat trout. Presumably, the trout in Pine Creek are descendants of the cutthroat that were introduced into Spring Valley in 1876, reportedly from Trout Creek, Utah. Two specimens from Trout Creek in the University of Utah examined by one of us (R. R. M.) are indeed of the same type as those from Pine Creek. Two cutthroat trout from Lehman Creek (UMMZ 141701, taken at about 8,000 feet in 1938), on the east (Bonneville) slope of Mt. Wheeler, closely resemble the Pine Creek trout and represent the native, probably undescribed, subspecies. In 1960, 1969, and 1970 Goshute Creek, tributary to Steptoe Valley, in the Cherry Creek Range, was stocked with the Pine Creek trout, after a cloudburst on August 5, 1955 had scoured the stream, eliminating the progeny of the 25,000 Yellowstone cutthroat trout that had been planted in the creek on September 11, 1953 (James Yoakum, personal communication, November, 1972).

Similar testimony published by Miller and Alcorn (1946, p. 175) specifies the transfer in 1873 of trout ("*S. c. henshawi*") across the Toiyabe Range from Reese River tributaries to Kingston Creek in Big Smoky Valley (the site of pluvial Lake Toiyabe), from which that type of cutthroat trout was stocked in Grass Valley (pluvial Lake Gilbert basin) and in Stoneberger and Roberts creeks in the drainage basin of ancient Lake Diamond.

More recently the Yellowstone cutthroat trout, *S. c. lewisi*, as well as the Lahontan cutthroat trout, *S. c. henshawi*, has been extensively stocked in mountain streams across Nevada (Miller and Alcorn, 1946, pp. 175–178; La Rivers and Trelease, 1952, p. 114; La Rivers, 1962, pp. 14, 18, 25, 31, 64, 90, 123, 138, 174, 184, 185, 275–300, 645–646).

We have failed, in repeated efforts, to find any indication that trout were native in any of the mountain streams on the east slope of the lofty Ruby and East Humboldt ranges, or elsewhere in the drainage basins of pluvial lakes Franklin and Clover, though they were no doubt native in the longer, lower-gradient streams, and lakes, on the western slope, in the Humboldt River system. Robert J. Behnke (personal communication, 1969) has accumulated confirmatory indications. The short, steep-gradient streams on the east side, in U-shaped valleys that held major montane glaciers almost unique in the Great Basin (Sharp, 1938), were apparently unsuited to the maintenance or survival of trout. This circumstance is closely analogous to the lack of native trout in Owens Valley, California, in the formerly glaciated valleys on the eastern escarpment of the Sierra Nevada.

We have similarly failed to locate from any source any evidence that trout are or have been native in the basins of any of the other pluvial lakes under study.

Salmo aguabonita Jordan.

Golden trout have been stocked in Nevada (Miller and Alcorn, 1946, p. 189; La Rivers and Trelease, 1952, p. 121; La Rivers, 1962, pp. 199, 317–318), with reported "good results" in Ruby Mountain lakes in Elko County. Those lakes are in the Humboldt River drainage basin, but La Rivers indicated (p. 318) that "officials hope to utilize this site as a stocking source for other waters in the mountains of Elko County."

Salmo gairdnerii Richardson.

Paleohydrography: pp. 18 (Bailey Ranch in Diamond Valley), 55 (near Currie in Goshute Valley), 58 (Steptoe Valley).

Locations: R9 (Grass Valley), G10 (Fish Creek Springs). Collection: 19 (near Currie).

Also in discussion of springs on Murphy Ranch in Steptoe Valley (p. 58) and of pools and springs in Spring Valley (p. 234).

All three treatises on introductions into Nevada document the widespread stockings of rainbow trout in the state.

Salvelinus fontinalis (Mitchill).

Paleohydrography: pp. 55 (near Currie), 58 (Steptoe Valley).

Locations and Collections same as for *Salmo gairdnerii*.

The extensive introductions into Nevada of brook trout are likewise specified in the three papers just mentioned.

Other Species

Coregonus clupeaformis clupeaformis (Mitchill).

In 1880, during the orgy of rampant introductions, 25,000 eggs of the Great Lakes whitefish were sent to Eureka, but no records of plantings seem available (Miller and Alcorn, 1946, p. 188).

Thymallus signifer tricolor Cope.

Grayling were unsuccessfully stocked in Ruby Valley in the 1940's (Miller and Alcorn, 1946, pp. 187–188; La Rivers, 1962, p. 200).

Cyprinus carpio Linnaeus.

Paleohydrography: pp. 46 (Butte Valley), 58 (Steptoe Valley), 66 (Geyser Ranch, Lake Valley).

Locations: R12 and G11 (Independence Valley), G9 (Warm Springs, Newark Valley). Collections: 14 (Stratton Ranch in Butte Valley), 22 (Campbell Ranch, Steptoe Valley), 23 (Steptoe Ranch, Steptoe Valley).
Also in discussion of pools and springs in Spring Valley (p. 234).

The introduction of carp into Nevada, with early enthusiasm and later disillusionment, has been chronicled by Miller and Alcorn (1946, pp. 180–181), La Rivers and Trelease (1952, p. 116), and La Rivers (1962, pp. 18–21, 448–453, 525).

Carassius auratus (Linnaeus).

Paleohydrography: p. 18 (Big Shipley Spring in Diamond Valley).
Location: R8 (Big Shipley Spring). Collections: 22 (Campbell Ranch), 23 (Steptoe Ranch), 25 (Dairy Ranch)—all three in Steptoe Valley.
Also in discussions of Cherry and Schell creeks, Steptoe Valley (pp. 206–207).

Establishments of goldfish have been recorded by Miller and Alcorn (1946, pp. 181–182), La Rivers and Trelease (1952, p. 116), and La Rivers (1962, pp. 454–456), from several places in Nevada, some of which we have confirmed.

Ictalurus (Ameiurus) species.

Location: G9 (Warm Springs, Newark Valley).

This report on "catfish," presumably of this subgenus, and one of "bullheads" in "Lake Donpah-gate" in Diamond Valley (p. 17), are the only ones we have obtained for the study area. We have collected bullheads elsewhere in Nevada, for example *I. n. nebulosus* (Lesueur) from Humboldt River near Carlin (G3) and *I. m. melas* (Rafinesque) from that station and from Carson River near Fallon (G1). The establishment of these and other ictalurids in Nevada has been treated by Miller and Alcorn (1946, pp. 182–184), La Rivers and Trelease (1952, p. 118), and La Rivers (1962, pp. 18, 479–497, 647–649). For our study area, La Rivers (pp. 648–649) listed *I. nebulosus* from Flynn Pond in Diamond Valley, Bassett Lake in Steptoe Valley, and Warm Springs Pond in Newark Valley.

Perca flavescens (Mitchill).

The only report of the yellow perch being introduced into the present study area is one for Bassett Lake in Steptoe Valley (La Rivers, 1962, p. 649).

Micropterus salmoides salmoides (Lacépède).

Paleohydrography: pp. 45 (Ruby Valley), 60 (Comins Lake).
Locations: R4 (Ruby Valley), R12 and G11 (Independence Valley). Collection: 20 (Cardano Ranch, Steptoe Valley).
Also in discussion of Ruby Lake (p. 198), of springs on Murphy Ranch in Steptoe Valley (p. 206), and of pools and springs in Spring Valley (p. 234).

The introduction into Nevada of largemouth bass, all we assume of the slower-growing northern subspecies (Bailey and Hubbs, 1949), has been detailed by Miller and Alcorn (1946, pp. 185–186), La Rivers and Trelease (1952, p. 119), and La Rivers (1962, pp. 24, 432, 554–560, 649–650).

Lepomis macrochirus macrochirus Rafinesque.

Bluegills, presumably all of the nominotypic northern subspecies, have been introduced into various parts of Nevada, particularly in the Humboldt River system and in Lake Mead, but in our area of special study we did not encounter any sunfish, and the only record we have found for that area is for Bassett Lake in Steptoe Valley (La Rivers, 1962, p. 651).

Archoplites interruptus (Girard).

Paleohydrography: p. 58 (Steptoe Valley).
Collection: 24 (Grass Springs on Lusetti Ranch in Steptoe Valley).
Also mentioned in discussion of pools and springs in Spring Valley (p. 234).

The Sacramento perch, the only native western member of the sunfish family, Centrarchidae, has become scarce in the Central Valley of California but has become common in some localities in the Great Basin, into which it was transplanted long ago (Miller and Alcorn, 1946, pp. 186–187; La Rivers and Trelease, 1952, p. 120; La Rivers, 1962, pp. 17, 18, 21, 545–553, 651).

For the area under special study, Miller and Alcorn (p. 187) reported that in August, 1938, the species was common "in a lowland slough at Lusetti Ranch, about 16 miles north of Ely." This report was based on local testimony received by the senior author at Ely on August 22, 1938, from the local game warden, Earl Mangum, who stated that he had transported many of these fish to other localities in Nevada, including No. 1 Well in Railroad Valley and Preston and Lund in White River Valley. In 1962, James E. Deacon (personal communication, 1965) found the species persisting in a larger spring, on Lusetti Ranch, where it apparently had extirpated *Relictus solitarius*, which held out in three smaller springs not containing the predaceous centrarchid.

On August 22, 1938, John Yelland (see p. 231) indicated that this fish had succeeded marvellously well, even in the brackish lakes of Spring Valley. La Rivers (1962, p. 549) had information that the species had died in this valley during a severe drought. He added that there was a substantial but stunted population in Bassett Lake in Steptoe Valley. His list of localities for the species in Nevada (p. 651) included Bassett Lake in Steptoe Valley and Little Meadow Lake in Spring Valley.

Although this species has proved predatory on a native minnow in Nevada, it is itself vulnerable to predation, because it does not guard its eggs. It has proved to be resistant to high-salinity waters, in general as well as in Spring Valley, and it is being extensively and successfully stocked in such waters (McCarraher and Gregory, 1970).

Pomoxis nigromaculatus (Lesueur).

The only record of the black crappie found from our study area is that for Fish Creek in Little Smoky Valley (La Rivers, 1962, p. 652).

SURVIVAL AND CONSERVATION

The studies that we and an increasing number of colleagues have been conducting on the hydrography and ichthyology of the Great Basin and other arid parts of the American West have highlighted the peril that the fishes of the remnant waters have faced and continue to face. Several species and subspecies that had maintained existence over the millennia since late Pleistocene time of more ample water have become extinct during the past few years through the deterioration of their environment, and others are on the verge of oblivion. It was our dubious privilege of describing posthumously (Miller and Hubbs, 1960) a species and a subspecies of peculiar minnows of the Colorado River system that had failed to survive the perils they had met during the two decades between their discovery and their description. More recently, we have added another posthumous description, that of *Rhinichthys osculus reliquus* (Hubbs and Miller, 1972, pp. 104–105), here treated. Several other endemic fishes of the arid West, and even one entire genus (*Empetrichthys*), have become endangered, and are being recognized as such in the international and U.S. federal 'Red Books' (referred to by Miller, 1972). Some of the documentation has been provided by Miller and Hubbs, 1960; Miller, 1961, 1968, 1969, 1972; Deacon, Hubbs, and Zahuranec, 1964; Hubbs and Deacon, 1965; Minckley and Deacon, 1968; Bunnell, 1970; Deacon and Bunnell, 1970; Miller and Pister, 1971; Miller, 1972, 1973; Pister, in press.

It is true that mass extinction has been the rule over the millennia of aridity, as is stressed above (pp. 74–76). It is, therefore, small wonder that some subspecies and species have succumbed to the stress inflicted by man on their fragile habitats, while others have reached the endangered category. However, it is also true that the survivors have become almost unbelievably resistant to desiccation, and through speciation during isolation have to some degree actually increased in number of subspecies. The very persistence of certain species and their speciation have bestowed upon the remnant forms a particular value and interest.

The peril of existence has accelerated as the miniscule habitats of the fishes of the north-central Great Basin have been degraded or at times have

even been eliminated by human activities, notably by the overuse of the waters for agriculture—usually marginal or often submarginal. As we have repeatedly documented in this report, habitat deterioration and threat to survival have been effected by diversion of water, by ditching, even by piping the entire waterflow, by removal of vegetation, and, disastrously at times, by the lowering of the fossil ground water through overpumping ('water mining').

Another ominous threat to the survival of the native fishes in the area under special treatment, and in other western regions, has been the widespread introduction of exotic fishes and other animals, including the frequently introduced and established bullfrog, *Rana catesbeiana*, a probable fish predator. Most of these introductions have been of species native to the faunally rich ecosystems of the eastern United States, wherein competition and predation have been highly evolved, whereas the native fishes of the isolated and faunally depauperate western waters have largely lost their ability to compete and to evade predation. In addition it may well be that the isolated native fishes have not developed, or have lost, immunity to parasites and diseases that the introduced species disseminate; for example, a case of parasitism affecting a native fish of southern Nevada, *Crenichthys baileyi* (pp. 227–228), has been attributed, with appropriate timing, to the introduction of exotic aquarium cyprinodonts (Wilson, Deacon, and Bradley, 1966).

The occurrences of exotic fishes are mentioned under the pertinent Locations for *Rhinichthys* and *Gila* and under the Collections for *Relictus*, and the introductions of the exotics are further treated in systematic order (pp. 235–240). Three species not native to any of the 21 pluvial lake basins under detailed study, namely *Catostomus platyrhynchus*, *Richardsonius egregius*, and *Gila atraria*, are treated among interbasin transfers (pp. 229–235). Of these the first two have seemingly not persisted where stocked. *Gila atraria*, the Utah chub, has become established in four of the basins under study (pp. 58, 60, 64, 66), wherein it has, as in some other places, increased inordinately in abundance.

Fortunately, the area of special study has largely escaped the establishment, purposely or otherwise, of tropical home-aquarium fishes, such as has taken place, at an ominously increasing rate, in the southern parts of Nevada and California. Our special area has apparently also escaped, at least largely, the establishment of the mosquitofish, *Gambusia affinis* (Baird and Girard), which Miller and Hubbs (1960, pp. 22–28), Myers (1965), and others, have regarded as constituting a significant danger to the native fishes, largely through the consumption of fry.

Survival Status Of The Endemic Fishes

We now briefly review, in systematic sequence, the survival status of each of the species and subspecies of endemic fishes of the north-central area of the Great Basin under present study. As noted in the preceding section on Transfers of Great Basin Fishes certain species of desert fishes exotic to the area under treatment have been stocked in refugium ponds in Spring Valley.

Speckled Dace, *Rhinichthys osculus*.

Although one of the three subspecies of speckled dace that we have described appears to have become extinct in the past few years, and the other two have been hovering on the brink, the species as a whole, as we interpret it, can not be regarded as endangered, for it lives in a multitude of habitats over a great part of the American West. Many other subspecies, some named and others not, are no doubt also threatened.

Lahontan Speckled Dace, *Rhinichthys osculus robustus*. Some of the more or less distinctive local populations of *R. o. robustus* are probably endangered, but the subspecies, as we treat it, is of such common occurrence over such a broad area as not to be feared in danger. Of the local populations treated in this report, those of a single tiny spring in Carico Lake Valley and of Indian Creek in Crescent Valley (p. 106)

(both outside the basins of detailed study), may well be in danger. Presumably, various populations will survive in the Humboldt River headwaters. Of the five local populations in the basin of pluvial Lake Diamond, that of the warm spring on Potts Ranch was on the verge of extirpation during our examination in 1938 (as is detailed on p. 114) and may well be gone now. A very similar stock, however, has just been found persisting in the small stream fed by springs about Dianas Punch Bowl, in the same valley, a few miles to the southward, and it probably has been increasing in population because of ditching. We suppose that the Coils Creek, Big Shipley Spring, and Birch Ranch populations (pp. 114–115) still persist, though the stock in Big Shipley Spring in 1938 was apparently considerably reduced by modifications of the environment and perhaps by the establishment of goldfish. A sanctuary at Birch Ranch might save not only the slightly modified local form referred to *R. o. robustus* but also the more notably differentiated local endemic of *Gila bicolor* (pp. 154–156).

GRASS VALLEY SPECKLED DACE, *RHINICHTHYS OSCULUS RELIQUUS.* The evidence seems sound that this very distinct subspecies, which we found in 1938 confined to the spring area in Grass Valley, has since become extinct (pp. 121–128, 240). The factors seem to have been the agricultural use of the water and, particularly, the stocking of trout. The loss of this Ice Age relict is a tragedy. It was a relict of some Pleistocene time, probably prior to the last pluvial.

If a residual population of the subspecies should be found, it would be highly desirable to provide a sanctuary for it, either in Grass Valley or elsewhere.

CLOVER VALLEY SPECKLED DACE, *RHINICHTHYS OSCULUS OLIGOPORUS.* Near extinctions of the two known populations of this rather well differentiated subspecies seem to have resulted from agricultural practices inimical to the dace and from the stocking of trout in the impounded waters. Some form of protection seems highly desirable.

INDEPENDENCE VALLEY SPECKLED DACE, *RHINICHTHYS OSCULUS LETHOPORUS.* This subspecies, more distinct than its Clover Valley cousin, has been shown (pp. 134–135) to be extremely rare and, fortunately, secretive in dense vegetation. It has probably been reduced to a low population by the impoundment of the spring water and the introduction of predators, including black bass, carp, and bullfrogs. Chances for the survival of this interesting dwarf dace would be greatly increased if the predators could be removed from the spring area or if a sanctuary, preferably in the home area, could be provided, with a device to exclude reinvasion by bass and carp. The companion endemic, *Gila bicolor isolata*, could be granted an asylum in the same enclosure, for they have long been living together. It is strongly urged that this project be undertaken.

TUI CHUB, *GILA BICOLOR.*

The multiple local forms that we refer to this species are so many and so widespread as to calm any fears that the whole species is in danger of extermination, even though various local forms are definitely threatened. The apparently increasing trend for the creek (*G. b. obesa*) and lake (*G. b. pectinifer*) subspecies to hybridize, owing probably to a decrease of the available waters in both quantity and variety, renders desirable the perpetuation of some nearly pure types.

HUMBOLDT CREEK TUI CHUB, *GILA BICOLOR OBESA.* It hardly seems reasonable that this widespread, central type could be regarded as in danger, but some recent examinations of the Humboldt River (in 1969) indicated that it had dwindled markedly in abundance and in distribution in comparison with the findings of either the Lahontan survey of 1915 (Snyder, 1917) or our main operations of 1938 and 1942. It is to be hoped that at least some populations, such as that of Bishop Creek, may be saved. The remarkable several-step cline of races in the relatively short Humboldt River is almost unique and would be valuable to preserve if at all possible.

The very distinct race of Sulphur Spring in Diamond Valley that we refrained from according subspecies rank seems strictly confined to the head spring pool (p. 154) and therefore hangs on a delicate thread—if indeed it still survives. The nearby springs should be checked to see if there are other surviving pockets, and at least one population should receive protection, preferably in the home territory. Perhaps not quite so urgently, but still definitely, the spring head at Birch Ranch (pp. 115, 155) should be utilized as a competitor-free habitat for its endemic races of *Rhinichthys osculus robustus* and *Gila bicolor obesa*.

NEWARK VALLEY TUI CHUB, *GILA BICOLOR NEWARKENSIS*. This distinct subspecies presumably maintains some populations, in Newark Valley, though we have not rechecked them since our collections of 1934 (pp. 157, 160). A new survey is definitely in order. The delicate balance that such isolated stocks face was emphasized by the report we received of the complete die-off, through the freezing of a marsh area a few years before, of a population that had existed between the two main Locations sampled. Some competitor-free sanctuary, preferably at the type Location (G7), seems desirable.

FISH SPRINGS TUI CHUB, *GILA BICOLOR EUCHILA*. This noteworthy subspecies, which with *G. b. newarkensis* represents postglacial speciation, is certainly also worthy of secure protection —if, as seems highly probable, it still exists, as it did in 1938. The region of the type and only Location for this relict definitely appears to be the proper locale for a sanctuary.

INDEPENDENCE VALLEY TUI CHUB, *GILA BICOLOR ISOLATA*. This additional distinct, residual-endemic subspecies, which was discovered in 1965 and 1966 (pp. 134, 175–180) surely also deserves some form of adequate protection, along with its companion relict, *Rhinichthys osculus lethoporus*.

RELICT DACE, *RELICTUS SOLITARIUS*.

Although examples of local decrease in abundance and even of occasional local extirpation were encountered in our field work of 1934–71, this remarkable ancient relict seems to be, at least for some time, safe from complete extinction, in the spring-fed waters that it inhabits in the pluvial drainage basins of lakes Franklin and Gale, in Ruby and Butte valleys, and of lakes Waring and Steptoe, in Goshute and Steptoe valleys.

The one really catastrophic depletion of the populations of the relict dace has occurred in Ruby Valley proper, between our discovery of the species there in 1934, when it existed in vast numbers, and 1965–67, when it could be located in very small numbers in only a very few habitats that had not been penetrated by black bass and other exotic, predatory gamefishes, which abounded in the ponds representing Ruby Lake (pp. 197–199). It seems very doubtful that the probably slightly differentiated form of Ruby Valley can be saved, though it would be grand if a supply could be located to stock a spring area kept free of fish-predator invasion by the installation of a siphon outlet.

Fortunately a goodly supply of *Relictus* probably remains in the northern part of Butte Valley that has had pluvial and modern-flood connection with Ruby Valley. However, the local form there seems somewhat different (though not regarded as subspecifically separable) and it would be preferable to retain separately representative stocks of both Ruby and Butte valleys (and even from the Lake Franklin and Lake Gale divisions of Butte Valley). It would also serve science and conservation if sanctuaries could be built and maintained for the Johnson Ranch, Phalan Ranch, and above-Currie stocks of the Lake Waring basin, and for at least one, preferably several, stocks of *Relictus* in the basin of pluvial Lake Steptoe.

Testimonial evidence was received (pp. 202–207) of the former enormous, in part seasonal, abundance of *Relictus* in Steptoe Valley, and of occasional extirpations, as at Murphy Ranch, probably as the result of manipulations of the water supply and the introduction of trout and

Utah chubs. A few other instances of local elimination were indicated by testimony to have resulted from manipulation of water, from stocking with Sacramento perch, *Archoplites* (p. 239) and other predators, and from other causes. However, the survival of this relatively uniform, unique species does not seem to be in imminent peril.

Railroad Valley Springfish, *Crenichthys nevadae*.

There have been some signs or at least fears of the depletion of this remarkable endemic relict cyprinodont, which is restricted to two areas in Railroad Valley (pp. 227–229), but we have no evidence of its being in, or approaching, the endangered category. Nevertheless, its reliance on very limited warm springs places it in a precarious status. Fortunately, another population has already been successfully established by transplantation (p. 229). The species justifies a 'rare' rating, because of its few, very small habitats. The probably precarious status of the isolated populations of *Crenichthys baileyi*, the only other species of the genus, and the nearly complete extinction of the whole genus *Empetrichthys*, the only close relative of *Crenichthys*, need be kept in mind in planning for the perpetuation of *Crenichthys nevadae*.

Hopeful Signs Of Protection For Endangered Species Of Desert Fishes

Fortunately, in the current wave of awareness of the need for conservation, the plight of the endangered desert-spring fishes has become appreciated by federal and state fish and game departments, by the federal bureaus of Land Management and Reclamation, by the National Park Service, and by other agencies, as well as by biologists and conservationists. The Desert Fishes Council, made up of governmental employees, conservation agencies, and the concerned public, has emerged as a potent force. Positive actions to avert exterminations have been initiated, and the future appears less ominous. Such action has included the establishment of sanctuaries, with control of trespass and construction of devices to prevent reinvasion of exotic fishes (Miller and Pister, 1971); transplantations; and the prohibition of the use of springs for aquarium-fish rearing. Other vital steps include action to prevent the mining of ground water nearby; the withdrawal of public lands and the purchase of springs from private owners; and the inclusion of threatened species on the 'Red Book' lists of endangered animals.

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In this four-decade study we have been favored with the aid of almost countless persons. Geological and biological colleagues who have shared their knowledge and experience with us in our Great Basin studies are in large part listed in our earlier, general report (Hubbs and Miller,1948b, p. 120), in which we added a statement, still true: "In numbers beyond the possibility of listing, local, state, and federal employees, ranchers, prospectors and townfolk gave freely, in the generous spirit of the West, of help, advice, and information." In the same report we listed aides who assisted in the field and laboratory activities, prior to 1948.

We now select, for special mention, alphabetically, certain persons who particularly assisted us in our studies in the north-central Great Basin.

Robert J. Behnke shared with us conclusions from his studies on the native distribution of trout in the north-central Great Basin; he donated the second collection of *Gila bicolor isolata*, and he sent the extensive class report on this form written by one of his former students, Stephen Harold Berwick. Robert E. Brown provided specimens of and ecological data on a stock of *Rhinichthys osculus robustus* that he found in 1972 in a hot-spring outflow by Dianas Punch Bowl. In 1971, Donald R. Cain of the Ely District Office of the U. S. Bureau of Land Management provided two supplementary collections of *Relictus solitarius*, along with a

very welcome suggestion for the establishment of a preserve for this unique fish. Ted M. Cavender has indicated that his unpublished osteological studies of "*Hybopsis*" *crameri* justify its continued segregation as a genus, *Oregonichthys* (considered in the discussion of *Relictus*). Patrick Coffin, Nevada Department of Fish and Game, provided, with good data, the only known specimens of *Rhinichthys osculus robustus* from Carico Lake Valley. James E. Deacon, University of Nevada, Las Vegas, provided specimens that he collected in the area of study, along with ecological and other data; and he rendered other help.

Lee R. Dice loaned a 2-foot Paulin altimeter for our 1938 and 1942 trips. The second collection of *Gila bicolor isolata* was loaned by W. I. Follett (California Academy of Sciences). When he was a student, John Thomas Greenbank made counts and measurements for us on the many local forms of *Gila bicolor*. Thomas P. Lugaski, graduate student at the University of Nevada, Reno, shared some information derived from his current studies of the fishes in north and central Nevada. Ira La Rivers, University of Nevada, Reno, has shared local testimony regarding the extermination of *Rhinichthys osculus reliquus* in Grass Valley, and has otherwise assisted us. When he was Refuge Manager at the Ruby Lake Wildlife Refuge, Donald E. Lewis obtained collections of minnows in Ruby Valley and located information about introductions. The Nevada Department of Conservation and Natural Resources supplied copies of the water-resource reports of various valleys. Much information, advice, and encouragement has come from C. T. Snyder and associates of the United States Geological Survey in Menlo Park, California. Their proposal of the name "Lake Hubbs" is much appreciated. Robert H. Soulages, a biology student at University of California, Davis, who has extensively explored underground and surface waters in Nevada, has provided information regarding physiography, waters, and fishes in Roberts and Egan creeks and elsewhere in the state. Thomas J. Trelease, Chief of Fisheries, Nevada Department of Fish and Game, provided information on fish transfers and introductions, granted collecting permits, and otherwise assisted us. For the expert preparation of the karyotype of *Relictus solitarius* and for the pertinent interpretation and comparison, we are deeply grateful to Dr. Teruya Uyeno.

Among the long-time residents of Nevada who recounted their memory of the introduction of fishes into some places and of their native occurrence or absence elsewhere—without which data the early record would be blank—we gratefully mention John Yelland, for his trust-inspiring information on the introduction of trout (p. 237) and Utah chubs (p. 231), on the original habitat of the relict chub (p. 234), and on the presence or absence of other fishes. Another very informative resident, Jerome Phalan Stratton (pp. 199, 206, etc.), who grew up in Butte Valley, helped particularly on place names, on the habitats of the relict dace, and on the presence or absence of minnows in various basins. His information, like that of Mr. Yelland, is regarded as highly reliable, as it stemmed from long ranching experience, involving observations on the fish in various springs.

Among others who helped with local information were ranchers Campbell, W. J. Gardner, Ellen Vallee, and Mrs. Zubiri, all in Steptoe Valley; William McGill of Ely, Earl Mangum (local game warden at Ely), and Dale V. Lockard of the Nevada Fish and Game Department, all dealing with Steptoe Valley and the relict dace; Forest Ranger Crane, rancher George Potts, and graduate student Robert E. Brown, in Monitor Valley; rancher Jorge Jacobsen in Diamond Valley; ranchers Isador Sara in Fish Springs Valley, Billy Moore in Newark Valley, Vernon Westwood in Clover Valley, Bert Robison in Spring Valley; and Mr. Moorman at Illipah Creek in Jakes Valley; also Selar S. Hutchings of the Desert Range Station and Otto Fife of Beryl Junction, Utah, regarding Pine Valley. For other names see Index.

James Yoakum of the United States Bureau of Land Management, Dale V. Lockard, and other

participants in the meetings of the Desert Fishes Council, have provided information on the efforts being made to preserve endangered fish species in the region under treatment.

Frances Hubbs Miller typed and reviewed much of the initial manuscript, prepared the index, and helped in the field. Other members of our families have assisted, particularly in the field work. The final typing has been the task of Elizabeth Noble Shor, who has consistently provided editorial suggestions.

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SUPPLEMENTARY NOTE

Frequent reduction in occurrence of barbels in isolated spring populations of *Rhinichthys osculus* (in southwestern Oregon) has been noted by Bisson and Bond (Copeia, 1971, no. 2, pp. 274–275). A general trend may well be indicated (see p. 104).

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Contents

Preface

On June 12, 1984 a symposium convened by Dr. Luis Baptista and sponsored by the Pacific Division of the American Association for the Advancement of Science took place at the California Academy of Sciences in San Francisco. The subject of the symposium was the origin of flight in birds, a topic that has garnered considerable attention in the past decade and is still unresolved. Did the ancestors of birds live in trees or on the ground? What kinds of animals were they? What kinds of ecological and aerodynamic pressures led them to develop wings, spread them, and go aloft? How did they take off and land? What lines of evidence are important or even germane to the problem? The authors of the papers in this volume present their readers with a spectrum of considered opinion and experience. Each author treats the problem thoroughly and reasonably. Why then should there be so little agreement among them?

The lack of consensus on how birds learned to fly is hardly surprising, inasmuch as no one was present to witness the process 150 million years ago, and the experiment is hardly repeatable. What possible interest would any legitimate scientist have in an issue that is never likely to be proven one way or another? To answer that question is to delve far beyond the issue of bird flight, into the heart of what makes scientists tick. No inference is free of theory; no fact stands alone on a pedestal, immune from charges of interpretive bias. History occurs only once; many possible roads could have been taken, but only one was actually followed. We will never know exactly how birds began to fly, but that is only part of the issue. More at stake is the issue of how questions like this one should be approached.

In perusing this volume, an outside observer should keep in mind that what scientists think is often less interesting than why scientists think what they do. The approaches that these authors bring to their topic directly reflect their interests and training; it is not simply a matter of the available evidence. To a paleontologist, the evidence for the origin of flight in birds might lie largely within the available fossil record, despite its legendary incompleteness and its inability to answer many questions about the once-living animals now buried in the rocks. A biologist might be justifiably more self-satisfied with the potential of the living biota to answer such questions; but not all animals that once lived are now alive, and some questions must go without answers.

The present volume underscores the diversity of the evidence bearing on the question of the evolution of flight. Jacques Gauthier concentrates on the phylogenetic evidence that places the origin of birds squarely within the small carnivorous dinosaurs (Theropoda: Coelurosauria) of the Mesozoic Era. His cladistic approach, while perhaps not fully endorsed by all taxonomists, has the advantage of being explicit, hierarchical, and easily amenable to further testing. Using sets of shared derived characters successively nested within each other, Gauthier shows that birds are members, in turn, of the coelurosaurs, theropods, dinosaurs, and archosaurs (to mention only a few of the more familiar subdivisions of the evolutionary hierarchy). The nested sequence of shared derived characters shows us not only the relationships of birds, but the sequence by which they acquired those characteristics commonly associated with flight. It may be surprising to ornithologists that the reversed hallux, reversed pubis, bony sternum, fused clavicles, and sideways-flexing hand are not strictly avian characters. Rather, they evolved in the somewhat larger, terrestrial, predaceous theropod relatives of birds. This suggests to Gauthier, as it has to some other evolutionary biologists, that these characters evolved in a completely different functional context; that birds are not as distinct from other archosaurs as textbooks would have us believe; and that true "birdy-ness" is probably based on a much more restricted set of characteristics, mostly centered on flight itself.

Walter Bock, by contrast, takes an almost completely neobiological view of this problem. Acknowledging the manifold gaps in the fossil record, and the severe limitations of fossils in answering questions of physiology, behavior, and metabolism, Bock regards the precise ancestry of birds as not critical to the problem of the evolution of flight. He reasons that the living world offers far more information about adaptations and physiology, and so suggests instead that the evolutionary biologist construct a "pseudophylogeny" of known living forms that might reasonably be functionally intermediate between successive evolutionary steps in the transition from nonflight to flight. Reviewing the differences between the two major theories to account for the origin of flight (the cursorial or "from the ground up" theory, and the arboreal or "from the trees down" theory), Bock emphasizes the theoretical difficulties with the cursorial model, for which no good living prototypes exist, and advocates the arboreal model, for which living arboreal gliders may be regarded as suitable prototypes.

John Ostrom, like Gauthier, grounds his theory for the origin of flight (no pun intended) firmly in the phylogenetic basis for the origin of birds among small Mesozoic coelurosaurs. Reasoning that this group of animals must have been small, agile, cursorial predators, and noting the complete absence in *Archaeopteryx* (the earliest known fossil bird) of what we would recognize in living animals as arboreal specializations, Ostrom believes it is more consistent with the available evidence to hypothesize that birds evolved flight from the ground up. Ostrom is careful to avoid saying that protobirds could not have gotten into trees; he merely sees no evidence for arboreality. This contrasts with Bock's view that whether or not protobirds mainly lived in trees, they must have gotten up there to launch themselves into the air. The differing consequences of these views are clear. Bock believes that a gliding stage was necessary; Ostrom does not. Bock believes that protobirds must have been able to climb; Ostrom does not. Ostrom favors the model of Caple, Balda, and Willis that shows how a running, leaping protobird could have developed stability in long, outstretched protowings, and how the resulting incremental lift and control could have paved the way for active, flapping flight. Bock is unimpressed with this model, but favors the objections of Rayner and those of Norberg that the speeds at which an animal would have had to run along the ground to achieve the minimum power speed of flight is prohibitively high to be considered plausible.

The portion of the argument that hinges on characteristics necessary to sustain lift and motion through the air is covered by the preeminent biological aerodynamicist Colin Pennycuick. Pennycuick outlines the requirements of air travel, both aerodynamic and energetic, and suggests that arboreal gliding is a far easier way to begin flight than any reasonable alternative.

In his view, however, not all animals may have begun to fly in the same way, and he considers possible biological factors that may account for some of the observed differences among birds, bats, and pterosaurs.

Though consensus may not have been reached here on many of the major problems associated with the origin of flight, there is no question of the importance of the problem as a paradigm for the understanding of major evolutionary questions. Flight appears to be an enormously difficult adaptation to evolve, in the sense that only three groups of tetrapods have ever been known to do it, and no nonflapping groups living today are obviously on their way to active flight. Yet flight is energetically cheaper than other modes of terrestrial transportation. If it is so advantageous, why is it so rare? The phylogenetic, ecological, and functional evidence presented in this book may provide some of the answers. The papers given here represent a fair cross-section of the approaches and opinions current in modern biology that have been applied to this question. The debate will no doubt continue; some compromises in both inference and method will undoubtedly surface; some problems will remain unsolved and rankling. This book will have done its job if it educates the diverse audience for which it is intended—ornithologists, paleontologists, vertebrate biologists of all interests—in the current issues related to the origin of birds and their flight; and if it stimulates its readers to read and learn more about what we know, why we think as we do, and how our training influences our approaches to scientific problems. After all, the unsolved problems may only require a fresh look from a new perspective; and that, at least, is available to everyone.

Two recent books will also be of interest to readers of this volume. In 1984, an international symposium on *Archaeopteryx* was convened at Eichstätt, West Germany. The proceedings of that symposium were collected as short papers in a volume entitled *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, eds.), and published by the Freunde des JuraMuseums Eichstätt at the end of 1985. Another companion volume, for readers further interested in the aeronautical aspect, is *Vertebrate Flight: A bibliography to 1985,* compiled by Jeremy M. V. Rayner (University of Bristol Press, Bristol, England; 1985). The alphabetical bibliography is cross-indexed according to various topics dealing with flight and the vertebrates that have evolved it. These two books should serve as useful starting points for those interested in pursuing further the topics treated in the present book.

For making the symposium and its volume possible, I would like to thank and acknowledge several people. Luis Baptista organized the American Association for the Advancement of Science Symposium at which these talks were presented. Daphne Fautin coordinated the initial editing and reviewing chores and provided much sensible advice and comment. Sheridan Warrick and Katherine Ulrich, of the Academy's Publications Office, did a superb job of copy editing the manuscripts for clarity and consistency, and offered many useful suggestions. To these people, the reviewers, and the California Academy, the authors and I are most indebted.

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Saurischian Monophyly and the Origin of Birds

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And if the whole hind quarters from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the Dinosauria.

T. H. Huxley 1870*a*

Introduction

The origin of birds has long been of interest to evolutionary biologists. Darwin and his colleagues were well aware of the problem presented by the "embarrassing gap" between birds and other amniotes (Desmond 1984). Indeed, because birds appear so different from other tetrapods, it could be argued that next to the question of the origin of man, that of the origin of birds was one of the most serious impediments to a general acceptance of Darwin's concept of the transmutation of species. The precise relationships of birds remain controversial, although the hypothesis that birds are archosaurs is now widely accepted. One of the goals of this report is to show that this controversy has much less to do with the evidence than it does with philosophical issues regarding interpretations of the evidence. I believe that the simplest and most interesting interpretation of the limited evidence available to T. H. Huxley and his contemporaries was that birds are part of Dinosauria. One would have hoped that work subsequent to Huxley's would have been directed towards determining the precise position of birds within dinosaurs. However, for reasons that will be discussed below, this was not to be the case. In fact, Huxley's views on bird origins were largely abandoned for much of the twentieth century, and the phylogenetic relationships of birds remain a persistent controversy.

Among current hypotheses for the relationships of birds among amniotes, only three have been supported by shared apomorphies and thus can be considered legitimate hypotheses in a phylogenetic context. Simply stated, these hypotheses are: 1) birds are the sister-group of mammals; 2) birds are the sister-group of crocodiles; and 3) birds are dinosaurs. The last two hypotheses agree that birds are archosaurs. The third could be divided into competing subhypotheses regarding the precise position of birds within Dinosauria, but this need not concern us. The first two hypotheses will be briefly reviewed below, along with a summary of the history of the third alternative, the principal focus of this paper.

Early workers suggested hypotheses, such as that birds were derived from early pterosaurs (Owen 1875; Seeley 1881), or from "lizards"[1] (Vogt 1879, 1880), or from "thecodonts" (Broom 1913). These and other hypotheses of their kind are ill-advised because they violate a basic tenet of evolutionary theory; as Michael Ghiselin put it (pers. comm.), "only species speciate, genera do not generate." Leaving aside the objection to the idea that higher taxa can act as ancestors in the usual sense, these hypotheses suffer for other reasons.

The pterosaur-bird hypothesis never received much attention, and the bird-"lizard" proposition deservedly received even less in that it was based entirely on plesiomorphic resemblances (such as sharing a long tail). In light of current knowledge, many apomorphies shared by birds and pterosaurs are most parsimoniously interpreted as convergences, which explains why the similarities between birds and pterosaurs are seldom either detailed or general to both taxa. However, the analysis below reveals some evidence that could be interpreted as supporting a somewhat modified version of Owen and Seeley's hypothesis: namely, that pterosaurs might be most closely related to theropods as a whole and thus to the subgroup of theropods including birds. Martin (1983*a*:111) cited *Scleromochlus* as sharing "a remarkably high percentage of the features suggested to relate birds to coelurosaurs." Martin evidently was unaware that Huene (1914*a*, 1948, 1956) thought that *Scleromochlus* might be related to pterosaurs. A more explicit restatement of Huene's hypothesis, including additional corroborating evidence, may be found in Gauthier (1984) and Padian (1984).

The Thecodont-Bird Hypothesis

One of the oldest and most popular hypotheses for the origin of birds has been that they evolved from "pseudosuchians" (hereinafter referred to as the "thecodont" ancestry hypothesis). "Pseudosuchians" comprise a basal group within the basal group of archosaurs, the "thecodonts," from which all other archosaurs, including birds, are supposed to have evolved. This hypothesis has been the chief rival of the dinosaur hypothesis for much of the twentieth century. The "thecodont" ancestry hypothesis was proposed by workers who were impressed with two main objections to the dinosaur hypothesis: 1) "dinosaurs" were either morphologically too specialized or stratigraphically too late to have given rise to birds; 2) convergence could explain equally well the similarities shared by "dinosaurs" and birds.

The first objection is not without merit, but it addresses only part of the issue. It emphasizes the dearth of evidence for direct filial relations of birds among dinosaurs, but it ignores the abundant evidence supporting common ancestry. (Just because one's cousins are not one's ancestors does not mean that one is not related to them.)

The second objection to the dinosaur hypothesis is more sub-

[1] The use of quotation marks around a group name means that in this context that group is paraphyletic. Paraphyletic groups include an ancestor and some (but not all) of its descendants (e.g., "mammals" without humans, or "lizards" without snakes, which are more closely related to some "lizards" than other "lizards" are). Monophyletic groups include an ancestor and all of its descendants, and these are the only kinds of groups that are considered legitimate for phylogenetic analysis.

tle than the first but is equally misguided. It is possible that birds and "dinosaurs" are convergent on one another because of their bipedal habits, but this is not the same as having evidence to support such a claim. Simply invoking the possibility of convergence is not enough (e.g., Charig 1976*a*, *b*). Both homology and homoplasy are deductive concepts contingent upon accepting one of several phylogenetic hypotheses (Rieppel 1980); the apomorphies supporting the preferred hypothesis are considered synapomorphies and those supporting alternatives are considered nonhomologous (e.g., convergent). Thus, without an alternative hypothesis of relationship, it is not possible to recognize convergence. Moreover, one must accept a shared apomorphy as a potential synapomorphy; to assume otherwise at the outset simply makes the convergence argument invulnerable to test.

For example, one is able to reject the proposition that two taxa possessing an apomorphic, mesotarsal ankle joint shared a more recent common ancestor within Archosauria; one need only observe that a newly discovered sister-taxon of either one of these mesotarsal archosaurs displays the ancestral condition (assuming no reversals). Indeed, both the convergence and homology propositions would agree on the significance of finding a member of the ingroup with the ancestral condition (i.e., convergence). However, if one simply asserts that the mesotarsal condition arose convergently, this proposition would be immune to new data; that is to say, no matter how many times newly discovered members of the ingroup were found to possess mesotarsal joints, one could still say that the crucial fossil (i.e., the unknown common ancestor) with the ancestral condition has yet to be found. There is only one simple and informative explanation for the mesotarsal joints of the birdlike archosaurs, and that is homology. There is, however, no limit to how complex an alternative explanation might be; taken to its logical extreme, it might as well be argued that all 9,000 species of birds acquired their mesotarsal ankles convergently.

By the early twentieth century an apparent alternative, the hypothesis of "thecodont" origins, became fashionable, and accepting this thesis required accepting the convergence argument. The two objections listed above may have set the stage for acceptance of the "thecodont" origins hypothesis, but broad acceptance of this idea arose with the description of one of the earliest and most generalized archosaurs, *Euparkeria capensis.* Broom (1913) and Heilmann (1926) then had an archosaur that was so ancient and primitive that it enabled them to derive birds directly from such a stage in archosaur evolution without having to pass through dinosaurs.

If in fact birds were so related, then one would expect to find evidence that all dinosaurs shared a more recent common ancestor with one another than any of them did with birds. Heilmann (1926) may have recognized this necessity, because he noted that the dinosaurs then known lacked clavicles. This suggested that birds, which have clavicles, were plesiomorphic compared to dinosaurs in this respect, and must have diverged from other, more primitive archosaurs that retained clavicles. The single piece of evidence supporting the "thecodont" origins hypothesis was refuted in 1936 when clavicles were found in nonavian dinosaurs (see Part IV, character 58).

More importantly, the great weight of evidence marshalled by Heilmann (1926) provides clear evidence that birds are theropod dinosaurs. That is to say, even if Heilmann were correct in concluding that nonavian dinosaurs lacked clavicles, the weight of his evidence still favored the thesis that birds are dinosaurs. Heilmann ultimately rejected the evidence favoring the dinosaur hypothesis and concluded instead that birds diverged from other archosaurs prior to the origin of dinosaurs. Heilmann's decision appears to have been predicated on a strict interpretation of Dollo's law of the irreversibility of evolution. Granted, one would not expect a hummingbird to evolve back into *Archaeopteryx,* especially by exactly reversing the historical sequence leading from the latter to the former, but one stretches the point by concluding that if clavicles were lost then they could never be regained.

The inadequacies of the "thecodont" ancestry hypothesis are most clearly seen in its claim that birds arose from an unknown member of "Thecodontia." From a phylogenetic perspective, "Thecodontia" and Archosauria are diagnosed by the same synapomorphies. Thus, these taxa are redundant, and when one says that birds evolved from "thecodonts" one is simply reiterating that birds are part of Archosauria. To say that birds are archosaurs would be true regardless of whether or not they were most closely related to crocodiles, pterosaurs, ornithischians, or any other monophyletic group within archosaurs. Thus, the "thecodont" ancestry hypothesis cannot be considered a legitimate alternative to the mammal-bird, crocodile-bird, or dinosaur hypotheses. Moreover, the "thecodont" ancestry hypothesis is a red herring that has served to deflect interest in and examination of the legitimate hypotheses of bird origins.

For example, as recently as 1980, Tarsitano and Hecht argued that birds were derived from "advanced thecodonts" that lacked dermal armor and had a birdlike ankle joint. In fact, these and other attributes apply to *Lagosuchus,* pterosaurs, and all dinosaurs, including birds (see Appendix A). Tarsitano and Hecht's (1980:176, fig. 9) cladogram correctly depicted birds as part of this group, but it also made other claims that were unsupported by evidence. For example, their "Theropoda" and other "Saurischia" were shown to be most closely related within this group, with *Lagosuchus* as their sister-group, and birds as the sister-taxon of the *Lagosuchus*-"saurischian" group. With the exception of birds, however, they failed to diagnose these taxa and thus support their conclusions. A more accurate depiction of their results would have been a cladogram with an unresolved multichotomy from the level at which the characters "mesotarsus" and "unarmored" arose. This would have established that "thecodonts" are a paraphyletic group, and that birds are part of the unarmored, mesotarsal group of archosaurs. One is still left with the possibility that birds are more closely related to some members of this group than they are to others. Rather than address this issue, however, Tarsitano and Hecht (1980:177) opted instead to "await better thecodont material and studies." In so doing, they provided an example of how the use of paraphyletic groups as ancestors can deflect interest from evidence relevant to hypotheses of common ancestry.

In conclusion, because the "thecodont" ancestry hypothesis is at best redundant and at worst a red herring, I recommend that it be ignored by future workers; discovering phylogenetic relationships among the birdlike archosaurs is difficult enough without the further obfuscation afforded by relying on paraphyletic groups as ancestors.

The Mammal-Bird Hypothesis

According to Desmond (1975, 1979, 1984), Owen (1841) used Lamarck's three criteria of nervous, respiratory, and vascular

organization to argue that dinosaurs, like birds and mammals, ascended to the physiological heights on Nature's ladder. Owen could hardly have been driven to such a conclusion by the scant remains of the three dinosaurs then known. Indeed, Desmond argued that by raising these huge saurians to ordinal status, Owen could argue that the "reptilian type" had long ago reached its apex, and that it had subsequently "degenerated into a sorry swarm of lizards" (Desmond 1984:119). Thus, Owen's Dinosauria depended less on evidence than on his abhorrence of Progressivism; his ulterior motive in recognizing the taxon was "to add one more nail to the transmutationist coffin" (Desmond 1979:233).

Owen's hypothesis received little attention in the post-Darwinian era, but it has been revived recently by Gardiner (1982). I will not here offer an extensive criticism of Gardiner's work, which dealt with tetrapod phylogeny in general and not just with the relationships of birds. Rather, I will confine myself to more general criticisms and let the evidence discussed below speak to Gardiner's (1982:227) claim that the "detailed correspondence between mammals and birds far outweighs" synapomorphy schemes supporting alternative hypotheses.

Gardiner intended to discover the relationships of "various living tetrapod groups . . . to one another" (1982:208) through "consistent patterns of derived characters" (1982:228). His actual effort was somewhat less ambitious, however, for he reviewed only that evidence consistent with the conclusions of some pre-Darwinian comparative anatomists. Moreover, he appears to have overlooked much of the evidence pertinent to tetrapod classification gathered by comparative biologists in the post-Darwinian era. Leaving aside these oversights, and certain misinterpretations of the evidence, Gardiner must be applauded for summarizing the apomorphies shared by mammals and birds that are absent in other extant amniotes; his hypothesis at least marshalled evidence in an explicitly phylogenetic context, unlike the case of the "thecodont" ancestry hypotheses.

In view of Gardiner's sedulous pursuit of apomorphies shared by mammals and birds, it is curious that he uncovered only four shared apomorphies—the form of the heart, aortic arches, occipital condyle, and pattern of temporal fenestration—that might contradict his hypothesized close relationship between mammals and birds. As Gardiner's sources for this evidence reveal, however, his search for contrary evidence came to a virtual halt at the beginning of the twentieth century. Moreover, Gardiner claimed that he was unable to find a single unique feature shared by dinosaurs and birds (1982:222). In view of the evidence presented below, which summarizes only part of the relevant information already in the literature, it is difficult to comprehend his failure in this endeavor. Perhaps the problem resides in Gardiner's use of the term "unique"? But this cannot be the case because if one accepts the mammal-bird hypothesis, then endothermy is unique, but if one accepts an alternative, such as the crocodile-bird hypothesis, then endothermy is not unique. Thus, the term "unique" as used by Gardiner reflects a conclusion, rather than an observation, and it cannot be a complete explanation of his oversight.

Perhaps Gardiner, like Owen, pursued the question of avian relationships with an ulterior motive. By virtually ignoring evidence determinable in both fossil and Recent taxa, and by stressing instead only part of the evidence determinable exclusively in extant forms, Gardiner may have revealed his intent: he was considerably less interested in reviewing all the evidence than in chastizing post-Darwinian paleontology for what he viewed as its excessive influence on our views of tetrapod phylogeny. If Gardiner had been more faithful to his avowed goals as a comparative biologist, he would have made a more complete survey of the literature upon which the evidentiary basis of the traditional view rests. The evidence supporting the traditional view that birds are archosaurian diapsids is reason enough to understand why comparative biologists have long held that, although birds and mammals are "warm in the palm of the hand," their immediate common ancestor among amniotes was not.

The Crocodile-Bird Hypothesis

Few have doubted that birds and crocodiles are one another's nearest relatives among extant amniotes. But Walker (1972, 1974, 1977) went further by claiming that birds and crocodiles were most closely related even within archosaurs. Walker (pers. comm.) subsequently rejected this hypothesis in favor of the theropod dinosaur hypothesis, but the crocodile-bird hypothesis has received further attention from Whetstone and Martin (1979, 1981), Martin, Stewart, and Whetstone (1980), and Martin (1983*a*). Martin (1983*a*) listed thirty characters that had been used to support the crocodile-bird hypothesis, but he accepted Tarsitano and Hecht's (1980) argument that nearly half of them are plesiomorphic resemblances. Among the characters that he did not reject owing to obvious plesiomorphy are the following.

1) Bipartite quadrate articulation, with apomorphic attachments anteriorly with the prootic and laterosphenoid and posteriorly with the prootic (in that the quadrate cotylus lies at the anterior base of the paroccipur);
2) Fenestra pseudorotundum carrying the perilymphatic duct;
3) Foramen aerosum in mandible;
4) Periotic pneumatic cavities in dorsal, central, and rostral positions;
5) Two pneumatic cavities surrounding the cerebral carotid arteries;
6) Pneumatic quadrate;
7) Unserrated teeth;
8) Tooth crowns short, bluntly conical, and with triangular profile;
9) Constriction between crowns and roots of teeth;
10) Expanded bony root covered with cementum and connected to jaw by periodontal ligaments;
11) Oval or round resorption pit;
12) Replacement tooth tilts labially and its main development takes place within the pulp cavity of its predecessor;
13) Teeth implanted in open groove at least in young individuals; and
14) Lingual walls and septa of major tooth-bearing bones formed by extensions of dense bone.

With the possible exception of a foramen aerosum, at least some of the pneumatic sinuses in the skull, and characters 10, 13, and 14 among those related to tooth-form and implantation, these characters do not appear to have been present in Archosauria ancestrally. I have observed a foramen aerosum in the carnosaur theropods *Tyrannosaurus* and *Albertosaurus* in a form essentially identical to that of extant birds (and unlike that of crocodilians). Other archosaurs are reported to have a crocodilelike foramen aerosum. For example, Wellnhofer (1985) has

reported it in pterosaurs and J. Clark (pers. comm.) has observed this structure in the archaic archosaur *Euparkeria*. Thus, the distribution of this character among archosaurs indicates that it may be the ancestral condition. However, L. Witmer (pers. comm.) notes that this foramen is absent in *Deinonychus*. Further examination of other archosaurs must be undertaken to determine the level of synapomorphy, and subsequent history, of this character.

Martin (1983*a*) noted that the fenestra pseudorotundum in birds and crocodiles can be distinguished on developmental novelties from analogous structures that evolved independently in mammals on the one hand and squamates on the other (see Gauthier, Estes, and de Queiroz, in prep.). Identification of a fenestra pseudorotundum in fossils is complicated by the absence of soft anatomical and developmental evidence, and one is left only with such evidence as can be inferred from the bony cranium and endocasts. Unfortunately, there are few well prepared braincases preserved in a way that could provide an unambiguous conclusion regarding its presence or absence among archosaurs. According to Walker (1972, 1974, 1977, pers. comm.), fenestra pseudorotunda are absent in the extinct relatives of crocodylomorphs, the aetosaurs and parasuchians, so this fenestra appears to be absent in Archosauria ancestrally. However, Raath and Walker (pers. comm.) identified a fenestra pseudorotundum in the theropod *Syntarsus*. I have observed a small fenestra in the same part of the ear region that might be the fenestra pseudorotundum in another member of the *Syntarsus* clade, *Dilophosaurus* (see Ceratosauria below). This structure also appears to be present in one carnosaur, *Acrocanthosaurus,* although it is said to be absent in the carnosaur *Tyrannosaurus* (Whetstone and Martin 1979, 1981). However, L. Witmer (pers. comm.) also examined *Tyrannosaurus* and concluded that the fenestra pseudorotundum was present. Witmer and Martin (pers. comm.) used different criteria for recognition of this character, so further study will be necessary to resolve this issue. Fenestra pseudorotunda are also reported in troodontid, ornithomimid, and caenagnathid theropods (e.g., Barsbold 1983; Currie 1986*a, b*), all of which appear to be closer to birds than are either *Syntarsus-Dilophosaurus* or carnosaurs (see Coelurosauria below). Whetstone and Martin (1981) questioned these identifications, and not without reason, for it is difficult to distinguish this fenestra from others connected to the more (e.g., caenagnathid) or less (e.g., ornithomimid) extensive periotic pneumatic cavities in the crania of these theropods. Whetstone and Martin (1979, 1981) were unable to identify a fenestra pseudorotundum in an ankylosaur ornithischian or in hadrosaurian ornithopod ornithischians. However, Sues (1980) and Galton (1983) claimed that it was present at least in ornithopods ancestrally. Thus, there appears to be some question regarding the level(s) at which this synapomorphy arose within Archosauria. Finally, characters 1, 2, 4, 5, 9, and 13 do not appear to support an exclusive relationship between crocodiles and birds within Archosauria, because Currie (1986*a, b*) has recorded their presence in the theropod *Troodon* (=*Stenonychosaurus*).

Martin (1983*a*) noted that no one has argued that the ancestry of birds lies within crocodiles, only that they both share an "unknown common ancestor." Martin (1983*a*:111) argued that the crocodylomorph *Sphenosuchus* is not "as similar to birds as is the Crocodilia"; the common ancestor of birds and crocodiles, as so proposed, must lie within Crocodylomorpha. Unfortunately, this relationship has not been made explicit; birds have yet to be placed within a cladogram depicting their precise relationship among crocodylomorphs. Such an analysis must eventually be undertaken by the proponents of the crocodile-bird hypothesis in order to make their hypothesis more amenable to test. For example, in a preliminary phylogenetic analysis of crocodiles and their extinct relatives, Crocodylomorpha was diagnosed by 13 synapomorphies (Gauthier 1984). Of these, only 7 are present in birds, indicating that if birds are crocodylomorphs, the former diverged from within the latter after the acquisition of the first seven shared apomorphies but before the remaining 6 crocodylomorph characters appeared. Moreover, the 14 additional characters diagnostic of true crocodiles within Crocodylomorpha must have evolved later still. This raises questions regarding Martin's interpretations of the level of synapomorphy of several characters, among them being the characters in tooth form and implantation cited above. That is to say, the tooth form unique to crocodiles appeared within crocodylomorphs only after the evolution of an anterodorsally inclined quadratojugal that extends to the skull roof, a partial secondary palate formed by the maxillae, loss of the ventral process of the squamosal, loss of clavicles, ventromedial elongation of the coracoid, and development of a characteristic wrist joint involving an elongate and columnar radiale and ulnare. However, some crocodylomorphs, such as *Terrestrisuchus* (Crush 1984), possess all six of the characters listed above in addition to those shared by birds and other crocodylomorphs, indicating that it is closer to true crocodiles than are birds. The problem emerges in the presence of sharply pointed, serrated teeth in *Terrestrisuchus* that appear to be implanted and replaced as in Archosauria ancestrally. If, as these data suggest, *Terrestrisuchus* and true crocodiles are closer to one another than either is to birds, then the dental apomorphies shared by birds and part of Crocodylomorpha must have been acquired convergently. This class of problems faces several of the supposed bird-crocodile characters listed above. In order to recognize and come to grips with such cases of character discordance, however, one requires a more precisely stated hypothesis than that birds and crocodiles share "some unknown common ancestor" (Martin 1983*a*:111), because this would be true in any case under the traditional view that birds are archosaurs.

The Dinosaur Hypothesis

Huxley's dinosaur hypothesis found its roots in Haeckel (1866), who considered birds to be basically "reptilian," and in earlier work of his own (Huxley 1864, 1867) in which he concluded that birds were derivatives of "sauropsid reptiles." Huxley was joined in supporting a "dinosaurian" origin of birds by other comparative anatomists including Cope (1867), Schmidt (1874), Marsh (1877), Gegenbaur (1878), Williston (1879), W. K. Parker (1864), T. J. Parker (1882), Baur (1883, 1884, 1885, 1886), and Darwin (1872). Indeed, Huxley's proposed "dinosaurian affinities" of birds gained broad acceptance during the latter quarter of the nineteenth century, even among the ranks of those who where "at best indifferent to Darwin" (Desmond 1984: 132).

In Huxley's 1869 address before the Geological Society, he described the "ornithic peculiarities" of Dinosauria as opening

up "a very interesting field of inquiry" that inspired him to devote "all my disposable leisure during the winter of 1867–8" to discovering characters shared by "dinosaurs" and birds that are not also shared by "lizards" and crocodiles. During this time Huxley also set out to examine critically "the material in the British Museum in order to ascertain how far the peculiarities of Megalosaurus were common to the Dinosauria in general." Huxley (1868, 1870*a, b*) cited 35 characters as "evidence of the affinity between dinosaurian reptiles and birds." Of these the following 17 characters survive critical examination in light of our current knowledge.

1) The skeleton is hollow and lightly constructed.
2) The cervical vertebrae are elongate.
3) There are more than two sacral vertebrae.
4) The scapula is elongate and narrow.
5) The coracoid is short and rounded.
6) The ilium is prolonged anteroposteriorly.
7) The acetabulum is roofed above by a supracetabular buttress of the ilium.
8) The bony contribution of the ilium to the acetabulum is more or less replaced by membrane.
9) The ischium and pubis are much elongated.
10) The femur has a strong anterior trochanter.
11) The femur has a crest on the ventral face of the outer condyle that passes between the tibia and the fibula.
12) The proximal end of the tibia is produced anteriorly into a strong crest, which is bent outwardly, or towards the fibular side.
13) There is a crest on the lateral side of the proximal end of the tibia for attachment of the fibula.
14) The tibia has a fossa distally for the reception of the ascending process of the astragalus.
15) The fibula is gracile compared to the tibia, and its distal end is much smaller than the proximal.
16) The astragalus is compressed, its articulation with the tibia is concave proximally and it has a convex, pulleylike distal surface, and the disparity in size between the tibia and fibula is also reflected in the astragalus being much larger than the calcaneum.
17) An "ascending process" (the intermedium) more or less tightly connects the astragalus and tibia.

Only some of these characters can now be considered to have arisen in the immediate common ancestor of Dinosauria (see Appendix A). Nevertheless, all of them appeared within the subgroup of archosaurs containing birds and thus they speak against the crocodile-bird hypothesis. At first glance, the explanatory powers of the crocodile-bird versus dinosaur hypotheses do not appear to differ greatly in that the former is supported by 14 shared apomorphies and the latter by 17. One must bear in mind, however, that the dinosaur hypothesis was formulated over a century ago with a fraction of the evidence currently available (see Appendix A). Although the crocodile-bird hypothesis is based on current knowledge, there would have been no reason to accept it over the dinosaur hypothesis as it stood in 1870, and there is even less reason to do so now. Huxley (1870*b*) mistakenly claimed that the absence of clavicles was diagnostic of Dinosauria, but this did not deter him from hypothesizing a bird-"dinosaur" affinity. I doubt that he considered the matter in this way, but he was correct in his judgement to the extent that it would have been simpler to accept the reappearance of clavicles in birds than to accept convergence as an explanation for each of the seventeen characters listed above.

In the discussion following Huxley's presentation before the Geological Society in 1869, Seeley remarked that he "thought it possible that the peculiar structure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds" (Huxley 1870*a*:31). With this simple declaration arose the issue that was to become the bane of Huxley's hypothesis. Seeley suggested convergence as an alternative explanation for the apomorphies shared by "dinosaurs" and birds without proposing the requisite alternative hypothesis of relationship.

The assertion of convergence was to be heard time and again in the ensuing years (e.g., Mudge 1879; Dollo 1882, 1883; Dames 1884; Parker 1887; Furbringer 1888; Osborn 1900). What made matters worse was the rise of the "thecodont" ancestry hypothesis in the early part of the twentieth century (e.g., Broom 1913; Heilmann 1926); this hypothesis appeared to dignify the otherwise bald assertion of convergence. The error was compounded even further when the convergence argument was applied not only to bird origins but to the question of dinosaur monophyly as well. Pandora's box had been opened; if an erect, bipedal posture and gait arose convergently in dinosaurs and birds, then what was to forbid multiple evolutions of such adaptively significant characters? The demise of the dinosaur-bird hypothesis went hand in hand with the demise of dinosaur monophyly; if one accepted the nonparsimonious reasoning behind the hypothesis that birds were "derived independently" from "thecodonts," then why not accept the even less parsimonious hypothesis that each of the remaining dinosaurian groups were "derived independently" from "thecodonts" as well? I see nothing that would forbid the multiple evolution of "dinosaurian" characters, but what evidence indicated that this did in fact take place? Although a few researchers advocated the dinosaur hypothesis (e.g., Boas 1930), the "unknown ancestor," coupled with the convergence argument, enthralled most systematists (e.g., Simpson 1946; de Beer 1954; Romer 1966).

There was renewed interest in the origin of birds in the 1970's, beginning with the publications of Galton (1970), Walker (1972), and Ostrom (1973). Galton (1970) stressed one of the characters initially employed by Huxley (1870*a, b*)—a reversed pubis—to suggest that birds were "derived" from ornithischian dinosaurs. Upon introduction to Ostrom's (1973) evidence, Galton rejected the ornithischian hypothesis (e.g., Bakker and Galton 1974). Martin (1983*a*) suggested that the presence of a predentary bone in Hesperornithes and its inferred presence in *Ichthyornis* may be further evidence of an ornithischian-bird relationship. The absence of a predentary bone in *Archaeopteryx* and all other birds speaks against Martin's conclusion; even if ornithischians were the sister-group of birds, it would still be simpler to accept a predentary bone as diagnostic of a taxon including only *Ichthyornis* and Hesperornithes.

Just as *Euparkeria* spurred interest in the "thecodont" ancestry hypothesis, Ostrom's finds of a new and strikingly birdlike theropod, *Deinonychus antirrhopus* (Ostrom 1969*a, b*, 1974*b*, 1976*b*), revitalized the dinosaur hypothesis. Ostrom's (1973, 1974*a*, 1975*a, b*, 1976*a*) hypothesized "coelurosaurian" ancestry of birds could be viewed as an extension of Huxley's pro-

posal, since the theropod *Megalosaurus* figured prominently in Huxley's arguments. The two hypotheses differed, however, in that Huxley looked at "dinosaurs" in general as "intermediate" between "reptiles" and birds, while Ostrom sought the ancestry of birds among "coelurosaur theropods" alone and skirted the question of dinosaur monophyly.

Early workers found favorable comparisons between birds and "coelurosaurs," and these comparisons were ably reviewed by Heilmann (1926). Although Heilmann has been considered the champion of the "thecodont" hypothesis, his closing comment (1926:185) upon finishing his comparisons between birds and "coelurosaurs" was: "We have therefore reasons to hope that in a group of reptiles closely akin to the Coelurosaurs we shall be able to find an animal wholly without the shortcomings here indicated for a bird ancestor."

After Heilmann (1926), a few authors advocated a special bird-"coelurosaur" connection (e.g., Lowe 1935, 1944*a, b;* Holmgren 1955). As Ostrom (1976*a*) noted, however, their ideas received little attention because they saddled themselves with burdens—most notably avian polyphyly—that inspired others to reject their ideas out of hand (e.g., Simpson 1946; de Beer 1954). Ostrom's resurrection of the "coelurosaur" hypothesis met with wider acceptance (e.g., Bakker and Galton 1974; Thulborn 1975, 1984; Thulborn and Hamley 1982), although his hypothesis was not without critics (e.g., Walker 1977; Tarsitano and Hecht 1980; Martin 1983*a*). Many of the criticisms were centered on the interpretation of certain anatomical details in imperfectly preserved fossils. Perhaps more troubling was the continued reliance on the part of Ostrom's critics on the "thecodont" hypothesis and its henchman, convergence.

Ostrom considered birds to have "evolved from coelurosaurs." However, in a phylogenetic perspective Ostrom's use of "coelurosaur" is no more informative than the name Theropoda, because both names are diagnosible by the same synapomorphies (see Introduction to the Basic Taxa, below). Thus, the "coelurosaur" hypothesis was no more precisely stated than was the crocodile-bird hypothesis, in that it merely claimed that birds and "theropods" shared an unknown common ancestor. In failing to let his hypothesis accurately reflect the structure of his evidence, Ostrom opened himself to a variety of criticisms, most of which were only misinterpretations invited by the obfuscation of paraphyly. It is inappropriate to consider each of these criticisms at this time, and the reader is referred to the character discussions below for examples of the problems stemming from treating paraphyletic and monophyletic taxa as if they possessed the same properties (i.e., a unique history involving origin, diversification, extinction, etc.).

Another result of Ostrom's vague conclusions regarding the relationships of birds to other theropods was that some workers mistakenly concluded that birds and theropods might be sister-groups (e.g., Tarsitano and Hecht 1980; Thulborn and Hamley 1982). The imprecision in Ostrom's proposition was rectified by Padian (1982), who extracted the relevant evidence from Ostrom's works and arrayed it in an explicitly phylogenetic context. Padian's provisional reanalysis demonstrated that birds are more closely related to some "coelurosaurs" than they are to others; the conclusion that birds and theropods are sister-groups could not be extracted from Ostrom's evidence. On the contrary, birds are deeply imbedded within Theropoda, just as humans are deeply imbedded within the phylogenetic nexus of Mammalia.

Bakker and Galton (1974) integrated the hypotheses of Ostrom and Huxley and resurrected the concept of dinosaur monophyly. Their method of analysis was somewhat more rigorous than the Simpsonian "evolutionary systematics" of Ostrom, although they were also hampered by such paraphyletic taxa as "thecodonts" and "prosauropods." The essence of Bakker and Galton's (1974) argument was as follows.

1) Dinosaurs (including birds) shared apomorphies not also shared by "thecodonts" and were therefore monophyletic.
2) "Prosauropods" were a primitive grade of dinosaurs that bridged the gap between ornithischian and "saurischian" dinosaurs.
3) All dinosaurs, like modern birds, were active endotherms; the behavioral and physiological apomorphies shared by dinosaurs are important; Dinosauria should therefore be accorded Class status.

Bakker and Galton's paper inspired considerable controversy (e.g., Thulborn 1975; Charig 1976*b*). The most telling criticisms were directed to the second and third points. To be sure, the link between Bakker and Galton's evidence and the conclusion of endothermy was a bit tenuous. The question of categorical rank of Dinosauria is trivial; current methods of establishing taxonomic rank rely entirely upon the authority of a systematist's subjective notion of what constitutes an ideal Class, Order, etc., and such Platonic and typological notions are anachronistic at best. Charig's (1976*b*) criticisms of Bakker and Galton's second point were for the most part trenchant and insightful. However, although some of Thulborn's (1975) and Charig's (1976*b*) criticisms of the evidence supporting dinosaur monophyly were factually accurate, for the most part they did not bear on the question of dinosaur monophyly.

Most criticisms of the resurrected Dinosauria hypothesis fell into one of three classes: 1) saurischians and ornithischians are too different to be monophyletic, 2) some of the alleged dinosaur characters were in fact present in some "thecodonts," and 3) the rest of the characters are functionally related and they could have been acquired convergently. The first class of criticisms is beside the point. One may be different from one's siblings, yet still share the same parents; the differences between bats and whales do not preclude their being mammals any more than the differences between the postdentary bones of *Ophiacodon* and *Homo* indicate nonhomology. Criticisms in the second class only indicate that some "thecodonts" are closer to dinosaurs (including birds) than are others; thus, "Thecodontia" is paraphyletic. Such evidence may not support dinosaur monophyly, but it does not speak against it either. The third class of criticisms leveled at Bakker and Galton's evidence for dinosaur monophyly is exemplified by a quote from Charig (1976*b*:79): "Most of these dinosaurian character-states were obviously adaptations to the fully improved ('fully erect') posture and gait of the dinosaurs . . . which could easily have evolved several times over, in slightly different ways, in response to similar functional requirements."

We have now come full circle; the exchanges between Huxley and Seeley, and between Bakker and Galton on the one hand and Charig and Thulborn on the other, demonstrate that the

dinosaur controversy has not altered on this issue in over a century. This controversy has nothing to do with evidence, although it must be admitted that until Hennig 1966, it was not widely understood that ancestry, rather than overall similarity or dissimilarity, must be the basis of phylogenetic classification. Consequently, there is little to be gained from taking the position that the problems will be solved by finding more fossils. There are, after all, many more fossils now available than there were in Huxley's time, and they still have not forestalled the old objections. The implications are clear: if our understanding of bird origins is to progress, we ought to rid ourselves of typological thought, namely, paraphyletic "Thecodontia"; reserve hypotheses of convergence for cases of character discordance, without which there is nothing for the concept of convergence to explain; and remember that although the world has no obligation either to be simple or informative, our hypotheses had better be both (Beatty and Fink 1979). By following these precepts, issues in archosaur phylogeny can be brought into sharper focus.

Knowledge of theropod anatomy has increased vastly since Buckland described *Megalosaurus* in 1824. Unfortunately, this knowledge has not been translated into a deeper understanding of theropod phylogenetic relationships. This circumstance reflects, in part, that Theropoda has yet to be diagnosed on the basis of synapomorphies. Indeed, most workers have been content to define "theropods" as "primitive dinosaurs" or "carnivorous saurischians"; which is to say that theropods are those saurischians that are not sauropodomorphs, and saurischians are those dinosaurs that are not ornithischians. In order to bring these taxa into the phylogenetic system, and thereby address the question of the phylogenetic relationships of birds, it will first be necessary to determine which, if any, phylogenetic entities within Dinosauria might be parts of Saurischia and Theropoda.

Materials and Methods

For the most part, the specimens examined are listed in the Introduction to the Basic Taxa. However, the materials constituting the core of the analysis were *Segisaurus, Dilophosaurus,* casts of the skull of *Ceratosaurus,* and several undescribed specimens in the collections of the University of California Museum of Paleontology (UCMP); *Coelophysis* in the collections of the Museum of Northern Arizona (MNA), UCMP, and American Museum of Natural History (AMNH); *Procompsognathus* in the collections of the Staatliches Museum für Naturkunde, Stuttgart (SMNS); *Compsognathus* in the collections of the Bayerische Staatssammlung für Palaontologie und historische Geologie, Munich (BSP); and the comparative osteological collections of extant birds housed in the UCMP, the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), the California Academy of Sciences (CAS), and the University of Michigan Museum of Zoology (UMMZ). These data were supplemented by photographs and notes on virtually every taxon referred to nonavian theropods compiled by Samuel Welles and Robert Long. Information on character ontogenies was derived from the literature and from cleared and double-stained series of *Alligator, Gallus,* and *Podiceps occidentalis* (UMMZ), in addition to late embryos and juveniles of a few passerines (CAS and pers. coll.), and the hindlimbs of three tinamou embryos (MVZ). These data were supplemented by that derived from skeletons of a hatchling *Pterocnemia* (MVZ) and a juvenile *Apteryx* (UMMZ).

For the purposes of this work, ontogenies will be divided into four stages: embryos, juveniles, subadults, and fully adult/mature individuals. Embryos refer to prehatching individuals; juveniles include stages from hatchlings to nearly full-grown specimens (i.e., subadults); subadults are those individuals that are near to maximum size as is indicated by some, but not all, of the developmental events marking the cessation of growth (i.e., senility). As used here, the term "fully adult" makes no reference to sexual maturity, which may or may not be coincident with this stage in skeletal ontogeny. Individuals that have reached the terminal stage of ontogeny are referred to variously as fully adult, fully mature, or as having attained maximum adult size. Subadults may also be near or at maximum adult size, but they do not display the full suite of developmental events in the skeleton that mark the cessation of growth. The cessation of growth in theropods may be recognized by the following events in the skeleton: fusion between the axial intercentrum and atlantal centrum, and fusion of this compound structure to the axial centrum; fusion of neural arches to centra; fusion of the vertebral components of the sacrum; full ossification of distal tarsal II; and, at least in nonavian theropods aside from ratites, fusion of the scapula and coracoid. Some of these events may precede others; however, any specimen in which all of them are present is here considered to have attained maximum adult size. By this definition, there are few nonavian theropod fossils that have achieved maximum adult size (e.g., the type specimens of *Syntarsus rhodesiensis* and *Ceratosaurus nasicornis*). There are also few specimens that could be considered juveniles, and even these few represent approximately half-grown individuals (e.g., the type specimen of *Compsognathus longipes* and, contrary to Howgate's 1984 view, the Eichstätt specimen of *Archaeopteryx lithographica*).

The methods employed here are essentially those of Gauthier et al. (in prep.). Following the procedure of Maddison et al. (1984), at least two outgroups were employed to identify 84 apomorphic characters distributed among 2 or more of the 17 basic taxa (18 including outgroup) that were the subjects of this analysis (see Introduction to the Basic Taxa, Fig. 7, and Appendix B). These data were then analyzed with Swofford's Phylogenetic Analysis Using Parsimony (PAUP) program installed in the University of Michigan's Terminal System. The analysis was two-part; the first run included only the comparatively well known taxa whose interrelationships were the principal foci of this analysis (viz., Ornithischia, Sauropodomorpha, Ceratosauria, Carnosauria, Ornithomimidae, Deinonychosauria, and birds), and the second run included all taxa, including those for which we have relatively little information owing to incomplete preservation. The first run yielded a single cladogram depicting the most parsimonious interpretation of the phylogeny of the seven well-known dinosaur taxa (Fig. 8). This cladogram requires 94 evolutionary events to account for the distribution of 84 apomorphies among the seven taxa, thus yielding a consistency index of 89%; that is to say, the single tree so obtained represents a highly corroborated hypothesis of relationship. However, the second run, which included both the better known and less well known theropods, resulted in numerous, equally

parsimonious trees. Nevertheless, the sister-group relationship among the seven well-known taxa were consistent across all possible trees. The multiple trees obtained in the second run resulted from the missing data in the 10 less well known taxa. For example, let us say that Coelurosauria includes only three taxa: deinonychosaurs, birds, and *Hulsanpes perlei.* Only three of the 84 characters under review were determinable for *Hulsanpes,* and although these data indicate that it is a coelurosaur, they are moot on the point of its precise affinities within this taxon. The PAUP analysis is so constructed that it considers all possible positions that *Hulsanpes* could have among coelurosaurs (viz., it could be the sister-group of birds, deinonychosaurs, or a deinonychosaur-bird group) and thus yields three equally parsimonious cladograms for these three taxa. Of course, none of these cladograms is actually supported by any evidence observable in *Hulsanpes.* Thus, when one considers the added possibilities allowed by the very incomplete remains of the 10 less well known taxa, the source of the numerous possible trees becomes apparent. However, two critical points must be borne in mind: first, the relationships among the seven taxa for which there is more complete information remained unchanged, and second, the overwhelming majority of possible trees were in fact uninformative. Consequently, they were collapsed into a single consensus tree incorporating multichotomies stemming from the levels supported by observable characters (Fig. 9). The consensus tree required 99 evolutionary events to account for the distribution of 84 apomorphies among the 17 basic taxa, thus yielding a consistency index of 85%.

Following Gauthier et al. (in prep.), the classification used in this work was constructed according to the following five conventions.

1) Only monophyletic taxa including an ancestor and all of its descendants are recognized, and in no case will a demonstrably paraphyletic taxon be considered in this analysis. Ancestry, rather than overall similarity, must be the basis for a phylogenetic system. The single exception to this convention is the metataxon.

2) A new category, the metataxon, is employed for taxa for which there is no positive evidence for or against recency of common ancestry. Following the suggestion of M. Donoghue, metataxa are provisionally allowed in the classification and their uncertain status is denoted by an asterisk following the name. For example, as will be argued below, the monophyly or paraphyly of the five fossil skeletons and a single feather impression referred to the earliest bird, *Archaeopteryx lithographica**, has yet to be firmly established, and it is therefore accorded metataxon status.

3) Certain widely used names are standardized by restricting them to taxa whose monophyly among extant amniotes is firmly established. Accordingly, Archosauria is standardized by limiting this taxon to all the descendants of the most recent common ancestor of extant birds and crocodiles. And Aves is likewise restricted to all the descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae.

4) Although the spelling of current taxonomic names is retained, no formal categorical ranks are recognized and hierarchical relationships within taxa are expressed instead by branching diagrams. Categorical ranks such as Class, Order, Family, and Genus, will not be recognized in this work.

5) Except to preserve binomials, no redundant names will be recognized. Thus, although *Archaeopteryx lithographica** is retained, redundant taxa conveying nothing further about phylogenetic relationships, such as Archaeopterygidae, Archaeopterygiformes, or Saururae will be ignored.

Introduction to the Basic Taxa

This section defines and diagnoses the theropod taxa that are the subjects of the present analysis (For diagnoses and definitions of the other basic taxa, Sauropodomorpha and Ornithischia, and the outgroup taxa, see Appendix A). These diagnoses are not definitive; the basic taxa are assumed to be monophyletic, and the characters are listed merely to show that there is at least some basis for the assumption of monophyly in each case.

Several workers have described the conventional groupings of "Carnosauria" for large theropods and "Coelurosauria" for small theropods as inadequate in view of the observed variation among Theropoda (e.g., Colbert and Russell 1969; Ostrom 1969*b*). Accordingly, modern classifications emphasize less inclusive taxa, typically ranked as "families," and these units will, for the most part, serve as the basic taxa of this analysis. In a phylogenetic context, "Coelurosauria" and "Theropoda" are redundant in that they have traditionally been diagnosed by the same synapomorphies. Huene (1914*b*) originally defined "Coelurosauria" on the basis of plesiomorphic resemblances, such as their small size and long necks. In other words, they are theropods that are not carnosaurs. However, because Huene based the concept on "coelurids," some of which have synapomorphies of a particular subgroup of Theropoda that includes birds, Coelurosauria will be retained in a modified form (see below).

A principal goal of this work is an examination of the phylogenetic relationships within Theropoda, with particular attention to the relationships among the better known theropods here included in Ceratosauria (n. comb.), Carnosauria (n. comb.), Ornithomimidae (n. comb.), Deinonychosauria, and birds. For the sake of completeness, the distribution of the characters discussed will also be noted in less well known taxa such as *Procompsognathus triasicus**, *Liliensternus liliensterni**, *Ornitholestes hermanni**, *Coelurus fragilis**, *Compsognathus longipes, Microvenator celer**, *Saurornitholestes langstoni**, *Hulsanpes perlei,* Elmisauridae*, and Caenagnathidae. As the use of the asterisk indicates, several of these taxa have not been adequately diagnosed; they may indeed be different from other theropods, but until they are diagnosed on the basis of characters relevant to the question of monophyly (i.e., synapomorphies), their status as phylogenetic entities must remain suspect. The position of these generally poorly known taxa are not so critical to the goals of this analysis, and the reader is referred to the literature for more information (Marsh 1881*a;* Osborn 1903, 1917; Ostrom 1970, 1978, 1981; Sues 1978; Osmolska 1981, 1982; Barsbold 1983; Welles 1984).

The more inclusive basic taxa may be newly recognized, or they may differ in diagnosis and content from concepts employed by other researchers. Some of the synapomorphies I consider diagnostic of the basic taxa could only have been recognized as such after the completion of the analysis; they are added now for the sake of completeness and in no case would the monophyly of any of the basic taxa depend on such determinations.

Elmisauridae* Osmolska, 1981

TEMPORAL RANGE.—late Cretaceous.
INCLUDED TAXA.—*Chirostenotes pregracilis**, *Macrophalangia canadensis**, and *Elmisaurus rarus**.

DIAGNOSIS.—Based on personal observation of *Macrophalangia** and *Chirostenotes**, and on published descriptions of these taxa in Gilmore (1924), Sternberg (1932), and Osmolska (1981). These taxa are represented by scant and often noncomplementary remains. Indeed, none of the referred taxa have been adequately diagnosed, and they are so poorly known that Osmolska (1981) suggested that they might be synonymous. According to Currie (pers. comm.), however, *Elmisaurus** and *Chirostenotes** are sympatric in Alberta in the late Cretaceous. Currie and Russell are in the process of describing a partial skeleton, including hands and feet, of *Chirostenotes**. Preliminary results indicate that *Chirostenotes** and *Macrophalangia** might be based on the same species. This conclusion is tentative because there appear to be two "morphs," and it is not yet clear if these morphs result from sexual or taxonomic differences. To further complicate matters, each of the apomorphies shared by elmisaurids* is either matched in some other theropods, or it could be considered part of a transformation series that is taken to extreme in some group of theropods (e.g., proportions of manal digit I approach those of ornithomimids). More evidence will be necessary to address these issues, but for the present Osmolska's Elmisauridae* will be accepted as a metataxon. Following is a list of apomorphies shared by elmisaurids*; as suggested above, these apomorphies may or may not prove to be synapomorphies.

Metacarpal I elongate and slender; relatively elongate first and second phalanges of manal digit III; metatarsus elongate and narrow; metatarsal III pinched between metatarsals II and IV, the latter two contacting one another proximally in front of III (similar modifications of the hands and tarsus are present in ornithomimids, troodontids, and ornithurine birds).

Caenagnathidae Sternberg, 1940

TEMPORAL RANGE.—late Cretaceous.
INCLUDED TAXA.—*Caenagnathus collinsi*, *C. sternbergi*, and *Oviraptor philoceratops*.

DIAGNOSIS.—No one doubts the monophyly of these peculiarly specialized theropods (Osborn 1924*b;* Osmolska 1976; Barsbold 1983). Caenagnathids were once thought to be related to ornithomimids because both share edentulous, beaklike snouts, but more recent work suggests otherwise (Barsbold 1983, and see below). Caenagnathids have highly modified skulls, and there is very little information regarding their postcranial skeletons. Several new specimens have been discovered, but they have yet to be completely described and illustrated (Osmolska 1976; Barsbold 1983). Barsbold is currently engaged in a revision of this taxon based on new material including as many as three species of *Oviraptor*, and an adequate diagnosis of this taxon must await his findings.

Currie (pers. comm.) has informed me that *Caenagnathus* (known only from cranial material) and *Chirostenotes** (known only from postcranial material) might represent the same species. Moreover, Wilson and Currie (pers. comm.) have suggested that *Microvenator** might be a caenagnathid. These hypotheses are only tentative, but they are included because Currie and Wilson's observations indicate that *Microvenator**, elmisaurids*, and caenagnathids might be monophyletic; such possibilities should always be borne in mind when dealing with metataxa.

Ceratosauria Marsh, 1884*b* (n. comb.)

TEMPORAL RANGE.—late Triassic to late Jurassic.
INCLUDED TAXA.—*Ceratosaurus nasicornis*, *Syntarsus rhodesiensis*, *Coelophysis bauri*, *Segisaurus halli**, *Sarcosaurus woodi**, *Dilophosaurus wetherelli* (including UCMP 37302, 37303, and 77270), and some undescribed forms represented by UCMP 129618 (referred to *Coelophysis* by Padian, in press), UCMP 128659, and MNA V. 2623 (referred to *Syntarsus* by T. Rowe, pers. comm.).

DIAGNOSIS.—The initial basis for recognition of the monophyly of this taxon stemmed from Welles's (1984) observation that one specimen referred to *Dilophosaurus* (UCMP 77270) possessed a uniquely modified trochanteric shelf (=modified anterior trochanter: see photograph of *Sarcosaurus woodi** in Charig 1976*b*). T. Rowe later observed this apomorphy in *Segisaurus**, and we have since observed this and other shared apomorphies in all taxa here included in Ceratosauria.

The presence of the trochanteric shelf in only some ceratosaur specimens is perplexing. However, Colbert, Rowe, and Raath (pers. comm.) have separately observed the presence of two femoral types among the large series of *Coelophysis* and *Syntarsus*, a robust form in which the trochanteric shelf is developed in the form characteristic of ceratosaurs, and a gracile form in which the trochanteric shelf is less modified and more like that seen in dinosaurs ancestrally. Dimorphism in femoral form, along with other differences in proportions, have been attributed to sexual dimorphism.

Although it has appeared elsewhere in theropods, another synapomorphy of Ceratosauria is the fusion between distal tarsals 2 and 3 and their respective metatarsals (T. Rowe, pers. comm.; Raath 1969). Rowe (pers. comm.) has discovered additional synapomorphies of Ceratosauria, including the shape and prominence of the supracetabular shelf, a fibular groove on the proximal end of the lateral side of the fibula (e.g., Gilmore 1920, fig. 65C), and a prominent groove on the ventrolateral side of the fibular condyle of the femur. Rowe (pers. comm.) also noted that, with the possible exception of *Segisaurus**, all ceratosaurs have a narrower pubis than is seen in other theropods aside from birds. Because *Coelophysis* is one of the earliest theropods, its narrow pubis was thought to be diagnostic of Theropoda. However, this apomorphy is diagnostic of most, if not all, ceratosaurs, and a relatively broader pubis appears to be the ancestral condition for Theropoda (e.g., *Allosaurus*, Madsen 1976).

A more complete discussion of the evidence supporting monophyly of Ceratosauria will be presented elsewhere (Rowe, in prep.).

Carnosauria Huene, 1920 (n. comb.)

TEMPORAL RANGE.—late Jurassic to late Cretaceous.
INCLUDED TAXA.—*Allosaurus fragilis*, *Acrocanthosaurus atokensis*, *Indosaurus matleyi*, *Alectrosaurus olseni*, *Dryptosaurus aquilunguis*, *Albertosaurus sarcophagus*, *A. libratus*, *A. lancensis*, *Alioramus remotus*, *Daspletosaurus torosus*, *Indosuchus raptorius*, *Tarbosaurus bataar*, and *Tyrannosaurus rex*.

DIAGNOSIS.—Based primarily upon the series of *Allosaurus fragilis* as described by Madsen (1976) and *Albertosaurus libratus* as described by Lambe (1917) and Russell (1970). These data were supplemented by personal examination of *Allosaurus*,

Albertosaurus, and *Tyrannosaurus,* and the descriptions of carnosaurs published in Marsh (1896), Osborn (1905, 1906, 1912, 1917), Gilmore (1920), Matthew and Brown (1922), Janensch (1925), Sternberg (1932), Stovall and Langston (1950), Rozhdestvensky (1958, 1965), Walker (1964), Colbert and Russell (1969), Ostrom (1969*a*), Steel (1970), Galton and Jensen (1979), and Barsbold (1983).

The medium- to large-sized theropods such as *Megalosaurus** and *Eustreptospondylus** possess some carnosaurlike attributes. These taxa are examples of a pervasive problem in theropod phylogeny, namely, the "megalosaur" problem. *Megalosaurus** was the first dinosaur described, but it is represented by limited material with no diagnostic features distinguishing it from other large theropods. As the name implies, "megalosaurs" are larger theropods, and several of their apomorphies are probably size-related in that they are also seen in large ornithischians and sauropodomorphs (e.g., femur longer than tibia). In view of profound character discordance, it is more parsimonious to accept these shared apomorphies as examples of convergence between "megalosaurs" and large ornithischians or sauropodomorphs. When considering the "megalosaurs" and Carnosauria, however, the problem of distinguishing homology from convergence is more difficult. Carnosauria shares many apomorphies with a portion of Theropoda that includes extant birds, and these can hardly be considered size related (see below). The problem with "megalosaurs" is that they either do not have these apomorphies, or the appropriate portions of their skeletons are unknown. S. P. Welles is currently involved in a revision of the "megalosaurs," and until he has revised the alpha taxonomy of this confusing group of fossils, there is little point in considering them further.

Several carnosaur apomorphies listed below are also present in other medium to large theropods such as *Dilophosaurus* and *Ceratosaurus.* Among the size-related apomorphies are opisthocoelous cervicals, the greater length of the femur relative to the tibia, a robust skeleton, and enlarged neural spines and transverse processes in the trunk vertebrae. These attributes are seen in all large saurischians. Nevertheless, the taxa here included in Carnosauria possess corroborating synapomorphies in addition to those related to their size, and other large theropods, such as *Ceratosaurus* and *Dilophosaurus,* do not.

Carnosauria is distinguished from other Theropoda considered in this analysis in that it possesses the following synapomorphies: orbit dorsoventrally elongate and roughly keyhole-shaped (Fig. 1G, H); supraorbital crests in fully mature individuals (Fig. 1G, H); frontals and parietals narrow and very short; reduction of mandibular fenestra (Fig. 1G, H); further reduction of dentary overlap onto postdentary bones and mandibular symphysis (indicating improved intramandibular joint, Romer 1956); pronounced development of bony shelf below mandibular condyle on lateral surface of surangular, presumably associated with insertion of enlarged pterygoideus musculature (Fig. 1G, H); ilium expanded anterodorsally (Fig. 5D); strongly opisthocoelous cervical and anterior trunk vertebrae (convergent in penguins); digits II and III reduced in hand, especially the latter, which is shorter than digit I (Fig. 4L; analogous condition in ornithurine birds, but resulting from loss of phalanges); very robust postcranial skeleton with stout, relatively thick-walled long bones, shortened and stoutly constructed trunk and cervical vertebrae (especially in tyrannosaurids), and large neural spines and transverse processes throughout vertebral column.

Tyrannosauridae, including *Albertosaurus, Tarbosaurus,* and *Tyrannosaurus,* are further derived within this assemblage in that they have the following synapomorphies: lacrimal excludes frontal from orbit (Currie, in press *a, b*); enlarged surangular fenestra and pterygoideus shelf (Fig. 1H); ventral process of squamosal nearly horizontally oriented (Fig. 1H); postorbital and jugal massive and anteriorly directed postorbital reentrant into orbit (Fig. 1H); tooth row fails to reach posterior to antorbital fenestra (Fig. 1H); forelimb less than one-quarter of hindlimb length; wrist bones very reduced (convergent in ornithomimids); third manal digit reduced to no more than metacarpal splint; ascending process very broad, extends dorsally for nearly one-third height of astragalus + tibia (convergent in coelurosaurs); calcaneum very reduced; and proximal end of metatarsal III strongly constricted between metatarsals II and IV (convergent in ornithomimids, elmisaurids*, and *Hulsanpes*).

Ornithomimidae Marsh, 1890 (n. comb.: includes Deinocheiridae of Osmolska and Roniewicz, 1970)

Temporal Range.—late Jurassic to late Cretaceous.

Included Taxa.—*Elaphrosaurus bambergi, Archaeornithomimus asiaticus, Ornithomimus edmonticus, O. velox, O. sedens, Struthiomimus altus, Dromiceiomimus brevitertius, D. samueli, Gallimimus bullatus, Ingenia yanshini, Garudimimus brevipes,* and *Deinocheirus mirificis*

Diagnosis.—Based primarily upon *Gallimimus bullatus* as described by Osmolska et al. (1972) and data derived from Russell (1972). Additional evidence derived from personal observation of *Struthiomimus* and descriptions in Marsh (1890, 1896), Osborn (1917), Parks (1928, 1933), Gilmore (1920, 1933), Janensch (1925, 1929), Sternberg (1932, 1933, 1934), Ostrom (1969*a, b,* 1970, 1974*a,* 1976*b*), and Barsbold (1983). The diagnosis below is based on Upper Cretaceous ornithomimids, although more complete knowledge of Lower Cretaceous and Upper Jurassic taxa may alter it.

Cornified beak as indicated by form of unworn margins of edentulous, beaklike jaws (Fig. 1I; convergent in Caenagnathidae and modern birds); premaxilla enlarged and beaklike, broadly contacting nasal to exclude maxilla from external naris (Fig. 1I); secondary palate formed by premaxillae and maxillae; reduced jugal and ventrally elongate postorbital; reduced lower temporal fenestra; quadrate strongly inclined so that distal end lies far forward of proximal end; bulbous parasphenoid (also in Troodontidae, and to a lesser extent in birds); metacarpal I elongate and all digits of subequal length (Fig. 4M); carpus very reduced with poorly defined articular facets on individual carpals; terminal unguals less trenchant and recurved, with reduced basal tubera (suggesting loss of raptorial function for the hand); humerus lightly constructed and deltopectoral crest reduced; ischium ventrodistally recurved (Fig. 5E); metatarsus narrow, and elongate compared to tibia length; metatarsal III strongly pinched between metatarsal II and IV, barely contacting distal tarsals (analogous modifications of the metatarsus arose convergently in tyrannosaurid carnosaurs, elmisaurids*, ornithurine birds, and troodontids); pedal digits short and stout.

Deinonychosauria Colbert and Russell, 1969

Temporal Range.—early to late Cretaceous.
Included Taxa.—Troodontidae and Dromaeosauridae.

Diagnosis.—Modifications of the foot in general, and the second pedal digit in particular, indicate a raptorial function for the pes in Deinonychosauria (Colbert and Russell 1969; Ostrom 1969*a, b*). According to these authors, the subequal lengths of pedal digits III and IV, together with modification of the raptorial pedal digit II, indicate functional didactyly during locomotion. The ungual on pedal digit II bears a large, compressed, trenchant, strongly recurved, scimitarlike claw. The second phalanx is shortened and subequal to the first phalanx in length. Moreover, the second phalanx has a prominent heel posteroventrally, and its anterior and posterior articular surfaces allow increased digital excursion. Troodontids may not be the sister-group of dromaeosaurs (see Section V). This point is not clear, however, and following previous authors, this taxon is accepted on the basis of the shared apomorphic resemblances in their feet.

It is interesting to note that Osmolska (1982) argued that the form of the metatarso-phalangeal joint indicated that the second pedal digit functioned differently in troodontids (=saurornithoidids) and dromaeosaurs. This observation alone cannot be taken to indicate nonhomology, because the morphology of one could be a transformation of that seen in the other, or both could be transformations of some more general condition shared by their common ancestor. Troodontids vary in the degree to which the second pedal digit is modified (Russell, pers. comm.). For example, *Troodon* has a more specialized raptorial second pedal digit and is more like dromaeosaurs in this respect. However, the second pedal digit is less modified in other troodontids (Osmolska 1982; Barsbold 1977). The possible effects of age, size, and sex on the degree of development of these characters has yet to be determined. Information on the possible influence of these factors might be gained from extant cariamids, *Chunga* and *Cariama,* that have analogously modified second pedal digits; examination of the biological roles of their feet may also provide some insight into the function of the second pedal digit in Deinonychosauria. (Although the information was received too late to include in this analysis, Currie has informed me that there is some evidence for a possible troodontid-ornithomimid group; in light of this it would have been more appropriate to consider three separate basic taxa—1 *Dromaeosaurus,* 2 *Deinonychus-Velociraptor,* and 3 Troodontidae—rather than one, viz., Deinonychosauria.)

Troodontidae Gilmore, 1924
(=Saurornithoididae Barsbold, 1974)

Temporal Range.—late Cretaceous.
Included Taxa.—*Saurornithoides mongoliensis, S. junior,* and *Troodon formosus* (=*Stenonychosaurus inequalis* and *Pectinodon bakkeri* following Currie (in press *b*).

Diagnosis.—Based upon personal observation of casts of *Stenonychosaurus inequalis* and descriptions and comparisons of both this taxon and *Saurornithoides* in Osborn (1924*b*), Sternberg (1932), Colbert and Russell (1969), Russell (1969), Barsbold (1974, 1977, 1979, 1983), Sues (1978), Osmolska (1981, 1982), Russell and Seguin (1982), Currie (in press *a, b*), and Wilson and Currie (in press).

Barsbold (1974) separated *S. junior* from *S. mongoliensis* because the former is 1.3 times larger, has a few more teeth, and the specimens derive from different stratigraphic formations. More specimens may indeed reveal that they are different taxa. However, the differences between these specimens could reflect size and age; current evidence cannot exclude the possibility that *S. junior* is merely an adult of the smaller *S. mongoliensis* (Currie, in press *a, b* notes a similar size range for *Troodon*). Accordingly, these taxa will be considered synonymous in the following analysis.

Anteromedially inclined orbits, suggesting broadly overlapping visual fields; deep depression in braincase in region of middle ear cavity (see Currie, in press *a*); bulbous parasphenoidal rostrum (also present in ornithomimids and in a less modified form in some birds); small, closely spaced teeth with enlarged (also seen in some dromaeosaurs), distally hooked denticles on posterior margin, anterior denticles reduced or absent at least in the lower jaw; deep, narrow Meckelian fossa of dentary; additional caudal vertebrae incorporated into sacrum (six sacral vertebrae); rodlike metatarsus with proximally attenuate metatarsal III wedged between slender metatarsal II and robust metatarsal IV; metatarsals II and IV in contact anteriorly in front of proximal end of metatarsal III (also in elmisaurids* and ornithomimids); and tonguelike distal articular surface of metatarsal III.

Dromaeosauridae Matthew and Brown, 1922

Temporal Range.—early to late Cretaceous
Included Taxa.—*Dromaeosaurus albertensis, Deinonychus antirrhopus, Velociraptor mongoliensis,* and *Adasaurus mongoliensis*

Diagnosis.—Based primarily upon *Deinonychus* as described by Ostrom (1969*a, b,* 1974*b,* 1976*b*). Supplementary data derived from descriptions in Matthew and Brown (1922), Osborn (1924*b*), Colbert and Russell (1969), Barsbold (1976, 1977, 1979, 1983), Sues (1977, 1978), Bonaparte and Powell (1980), and casts of the plastotype of *Deinonychus.* Sues (1978) included *Saurornitholestes** in Dromaeosauridae, but he did so on the basis of plesiomorphic resemblances; until the evidence supporting this placement is made explicit, this taxon will be considered separately.

Prezygapophyses and haemal arches exceed length of caudal vertebrae (Fig. 2G); short metatarsus compared to femur length; peculiar ginglymoid structure of the distal ends of metatarsals II and III; deeply grooved distal ginglymus of metatarsal II.

Avialae (n. txn.)
(L.: *avis,* bird; *alae,* wings)

Temporal Range.—late Jurassic to Recent.
Included Taxa.—*Archaeopteryx lithographica** plus ornithurine birds

Diagnosis.—Based primarily upon *Archaeopteryx lithographica** as described by Heilmann (1926), de Beer (1954), Ostrom (1972, 1973, 1974*a, b,* 1975*a, b,* 1976*a*), Wellnhofer (1974), Tarsitano and Hecht (1980), Martin (1983*a, b*), Whetstone (1983) and upon personal observation of the Eichstätt specimen and casts of the London and Berlin specimens.

This new taxon, Avialae, is named so as not to violate the

classificatory conventions of this work, in which widely used names like Aves are restricted to living taxa in order to maximize stability and phylogenetic informativeness. Because of feathers and the presumed ability to fly, *Archaeopteryx** has always been considered a bird. This informal usage has been maintained above, and use of the informal term "bird" for this taxon will be continued in the following discussion. In a formal sense, however, "birds" and Aves will not be synonymous. The "winged theropods" included in Avialae possess the following synapomorphies distinguishing them from other Theropoda.

Premaxillae elongate, narrow, and more pointed anteriorly, with longer nasal processes; maxillary process of premaxilla reduced so that maxilla participates broadly in external naris (also in troodontids; Currie, in press *a*); enlarged brain/basicranium (temporal musculature fails to extend origin onto frontal bones); double-condyled quadrate displaced from distal position on opisthotic to more anteromedial position in contact with prootic (Currie, pers. comm. and Walker, pers. comm., disagree with Whetstone's interpretation of the quadrate; Currie notes the anterior displacement of the quadrate in troodontids, and Walker does not consider the quadrate to be double-condyled in *Archaeopteryx**); maxillary and dentary teeth reduced in size and number (or lost), with unserrated crowns and enlarged roots that completely enclose replacement teeth within them (see Howgate 1984, for an alternative view); robust furcula for hypertrophied flight musculature (Olson and Feduccia 1979); scapula with more or less prominent acromion process for ligamentous connection to clavicle (see Martin 1983*b*, for alternative view); length/breadth ratio of scapula at midlength exceeds nine (not in penguins) and scapula tapers distally; acrocoracoid tuberosity larger than in other coelurosaurs; coracoid enlarged and inflected posteromedially more so than in other coelurosaurs; very long forelimbs and hands (e.g., in *Archaeopteryx** forelimb is 120–140% of hindlimb length, and more than twice as long as distance between glenoid and acetabulum), with forearm more than 87% of humerus length and metacarpal II approaching or exceeding one-half of humerus length; ischium compressed and dorsoventrally deep; compared to other theropods, tibia, fibula, and metatarsals relatively more elongate with respect to femur, regardless of body size (metatarsals short in penguins and some other birds, J. Cracraft, pers. comm.); fibula attenuate distally, and may not extend to end of tibia; proximal tarsals fused to tibia-fibula and to one another in adults; distal tarsals and metatarsals fused at least distally in fully adult individuals (convergent in some ceratosaurs, elmisaurids*, and *Hulsanpes*); first pedal digit elongate and reversed (may be reversed in some extant birds, R. Storer, pers. comm.), metatarsal I attached on distal quarter of metatarsal II; tail reduced to no more than 23 free caudal vertebrae; feathers cover limbs and tail, feathers on lateral margins of tail and posterior margins of arms enlarged, curved, and asymmetrically vaned, indicating aerodynamic function (e.g., Feduccia and Tordoff 1979).

It is not certain that feathers are confined only to avialans among coelurosaurs. *Compsognathus* apparently lacks them (Ostrom 1978), so feathers appear to have been absent in coelurosaurs ancestrally. However, *Compsognathus* is the only nonavialan theropod that is preserved in an environment of deposition conducive to the preservation of feather impressions. Thus, future finds may demonstrate that feathers arose prior to the origin of birds.

As the use of the asterisk indicates, *Archaeopteryx lithographica** is here considered to possess no apomorphies that would not be expected in the common ancestor of all birds. Thus, the specimens referred to this taxon are placed here because of their geographic and stratigraphic occurrence and overall similarity. These specimens probably represent a single species, but such opinions should always be distinguished from those based on appropriate evidence. Notwithstanding the interesting possibilities suggested by Martin (1983*b*) and Howgate (1984), there is no unambiguous evidence indicating either paraphyly or monophyly, and these specimens will be referred to collectively as the metataxon *Archaeopteryx lithographica**. Because of its generalized morphology and stratigraphic position, the specimens of *Archaeopteryx** could be parts of an ancestral population that gave rise to all later birds. Hypotheses of ancestral status can only be weakly supported in that they are based on negative evidence. Nevertheless, there is no unequivocal evidence supporting the alternative hypothesis, that *Archaeopteryx** is monophyletic and thus not an ancestral bird.

Whetstone (1983) and Martin (1983*a*) suggested that, compared to other birds, the squamosal is either reduced or absent in *Archaeopteryx**. This interpretation is open to doubt in view of the preservation of the specimens with cranial material; each of the specimens was preserved such that upon separating the slabs, the skulls fractured between the main body of the skull and the lightly constructed elements surrounding the orbit and temporal fenestra. These authors contended that the squamosal was absent because there is no evidence for its sutural connection to the skull. This contention loses much of its force because these sutural surfaces are also absent in theropods in which the squamosal is known to be present (e.g., *Syntarsus;* M. A. Raath, pers. comm.). Under such circumstances, it is difficult to distinguish between absence and nonpreservation. If further finds corroborate the Whetstone-Martin hypothesis, then *Archaeopteryx** must be removed from metataxon status and its hypothesized ancestral position must be rejected.

In keeping with one of the goals of this work, namely to provide a relevant series of outgroups for phylogenetic analyses among the major groups of extant birds, two more taxa within Avialae will be defined and diagnosed below. They are not basic taxa in this analysis, but it is necessary to consider Ornithurae and Aves at this point because the concepts represented by these names as used in this study may differ from those employed by others.

Ornithurae is defined here in keeping with its original intent as a taxon encompassing all extant birds, as well as all other birds that are closer phylogenetically to extant birds than is *Archaeopteryx**. Having been supplanted by Neornithes (Gadow 1893), Ornithurae (Haeckel 1866) is seldom used in current ornithological literature; the obscurity of the name has saved it from the diversity of meanings that possible alternative names have developed, and Ornithurae is thus an appropriate name for this taxon. As here defined, however, Ornithurae is a more inclusive taxon containing Aves, which reverses the traditional hierarchical relationship between these taxa. The terms Neornithes and Carinatae are avoided because their ambiguous and, at times, contradictory meanings in avian systematics have laden them with too much historical baggage to be useful in this work.

Ornithurae is recognized by a host of flight-related modifi-

cations in the skeleton that distinguish it from other theropods, including *Archaeopteryx**. The modifications indicate that the immediate common ancestor of Ornithurae possessed not only an inherited ability to fly, but the capacity for sustained flight approaching that seen in extant birds. It also appears that the immediate common ancestor of ornithurine birds had already overcome the energetically most demanding aspect of flight in modern birds—to become airborne from a standing start.

About 60 species of birds have been described from sediments of Cretaceous age, but most of these species are too poorly known to contribute much to our understanding of avian phylogeny (Elzanowski 1983; Thulborn 1984). To simplify the following discussion, only *Ichthyornis* and Hesperornithes will be considered. Moreover, because of character discordance, and ambiguities in character interpretations stemming from the specialized hesperornith morphology, it is not clear whether Hesperornithes or *Ichthyornis* is more closely related to extant birds. The evidence presented below indicates that neither taxon belongs within any subgroup of extant birds. Indeed, there is some evidence, such as the detailed form of the intramandibular joint and the possible presence of a "predentary" bone in both taxa, indicating that *Ichthyornis* and Hesperornithes collectively constitute a sister-taxon of extant birds (Martin 1983*a*). It is beyond the scope of this work to address these questions, and Ornithurae will be diagnosed by synapomorphies that can be found in any two of the following three taxa, Hesperornithes, *Ichthyornis,* and extant birds. This approach assumes that the flightless, foot-propelled divers of Hesperornithes were derived from an ancestor possessing the full suite of characters diagnostic of Ornithurae. This may not be the case, but at least Hesperornithes do not retain an unmodified ancestral condition. For example, as diagnosed below, Ornithurae possess a keeled sternum; Hesperornithes do not possess a keel, but the morphology of its sternum is certainly derived with respect to the condition present in other dinosaurs.

Ornithurae Haeckel, 1866

Temporal Range.—lower Cretaceous (at least Albian Stage) to Recent.

Included Taxa.—Extant birds and all other taxa, such as *Ichthyornis* and Hesperornithes, that are closer to extant birds than is *Archaeopteryx**.

Diagnosis.—This taxon is based on evidence derived from Marsh (1880), Martin and Tate (1976), Elzanowski (1977, 1981), Martin and Bonner (1977), Martin and Stewart (1977), McDowell (1978), Whetstone and Martin (1979, 1981), Martin (1980, 1983*a, b,* 1984), Martin et al. (1980), Whetstone (1983), and Thulborn (1984).

Body of premaxillae fused, edentulous, and beaklike; nasal process of premaxilla extends over nasal to closely approach frontal; facial process of maxilla reduced and naris enlarged (resulting in loss of maxillary fenestra); descending process of nasal contacts premaxilla to exclude maxilla from narial margin; maxilla with prominent medial phalange in palate (=maxillopalatine); ectopterygoid absent; palatine and pterygoid narrow and articulating near level of braincase (contra McDowell's 1978 interpretation of palatine as anterior pterygoid; pers. comm. L. Witmer and K. Warheit); peg and socket articulation between jugal and lateral cotylus of quadrate; extensive mesethmoid ossification appears early in ontogeny and is exposed on skull roof between nasals in late embryos/neonates (this character is retained into adult stages in Hesperornithes [Martin, pers. comm.] and Ratitae [Pycraft 1900]); neck includes more than 9 vertebrae (convergent in Ornithomimidae, which have 10 cervicals—ornithurine birds have at least 13 cervicals ancestrally); anterior cervicals with moderately developed heterocoely (see below); prominent hypapophyses in posterior cervical and anterior trunk vertebrae; loss of hyposphene-hypantra intervertebral articulations; sacrum includes more than 5 vertebrae (convergent in troodontids, which have 6—ornithurine birds have at least 10); free portion of tail reduced to fewer than 16 vertebrae; absence of caudal zygapophyses; presence of pygostyle including variable number of coossified vertebrae (secondarily lost in some Hesperornithes and Tinami, and in most Ratitae); ossified uncinate processes (reversed in Anhimidae and megapods; R. Storer, pers. comm.); ossified (rather than calcified) ventral ribs attached to sternum (the last two characters may apply to a more inclusive taxon in that Ostrom [1969*b*] and Paul [1984*b*] identified ossified ventral ribs and uncinate processes in dromaeosaurs); absence of gastralia; enlarged and posteriorly displaced sternum, chondrogenic cells of which proliferate and migrate to form keel; appearance of new sternal ossification center, the lophosteon, arising in region of sternal keel; shoulder joint set posteriorly and dorsal to center of gravity; hollow scapula and coracoid articulate via scapular peg and coracoidal socket below level of coracoidal portion of glenoid (reversed in some flightless birds, such as Hesperornithes and Ratitae), and scapula and coracoid fail to fuse in adults (reversed in Ratitae); scapula long (exceeds length of 7 trunk vertebrae), narrow (length/breadth ratio at midlength exceeds 12), tapering distally, and scapula lies near to and parallel with vertebral column and closely approaches ilium posteriorly (these characters are reversed in flightless birds); coracoid long, slender, tapered at midlength, broad distally and in or near contact on midline, and articulate in prominent grooves along anterior edges of sternum, with prominent acromion process for articulation of clavicle (=triosseal canal; some aspects of coracoid form may reverse in flightless birds, such as Hesperornithes and Ratitae); prominent, conical, internal tuberosity on humerus separated from head by capital groove; ulna approximately twice as thick as radius and with nobs along posterior margin for flight feather attachment; ulna with semilunate articular surface distally (reversed in some flightless birds such as Hesperornithes and Ratitae); characteristic carpometacarpus in adults formed from coossification of some distal carpals and metacarpals, with metacarpals I, II, and III fused proximally, and II and III fused distally, second phalanx of digit II broad and flat, absence of two phalanges on digit III, clawed unguals usually absent in adults (various flightless birds have lost other manal elements, e.g., digit II is the only finger remaining in *Apteryx* and *Casuarius;* present interpretation contradicts digital homology proposed by Hinchliffe and Hecht 1984); pelvis fused in adults; prominent antitrochanter above acetabulum; preacetabular portions of ilia elongate, closely appressed on midline, and in contact with at least some sacral neural spines, but postacetabular portions widely separated (reversed in some ornithurines such as Hesperornithes, Ratitae, Gaviidae); absence of bipartite distal moities of ischium (see Fig. 5H, I); pubes and ischia widely separated on midline; pubis shortened, without expanded foot distally, and with prepubic process proximally (not in *Ichthyornis*); femur with deep rotular groove anterodistally and prominent fibular condyle; tibia with

cnemial epiphysis; tibia with prominent tendinal groove anterodistally; fibula short, not in contact with proximal tarsals; proximal tarsals, including ascending process, fused to one another and to tibia early in postnatal ontogeny; distal tarsals form metatarsal cap with intercondylar prominence (reduced or lost in Ratitae), and this cap fuses to metatarsals early in postnatal ontogeny; proximal end of metatarsal III posterior to and more or less compressed by metatarsals II and IV (as in troodontids, ornithomimids, tyrannosaurids, and elmisaurids*); coossification among metatarsals begins distally (rather than proximally); small foramina between proximal ends of metatarsals (not perforating metatarsus in Hesperornithes); loss of raptorial modifications of pedal digit II (see below); loss of pedal digit V in adult (convergent in some ornithomimids and perhaps caenagnathids).

Aves Linne, 1758

Temporal Range.—late Cretaceous to Recent.

Included Taxa.—Aves is here restricted to the taxon encompassing all descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae, as these taxa are diagnosed in Gauthier et al. (in prep.).

Diagnosis.—Based on data derived from Huxley (1867), Pycraft (1900), de Beer (1956), Bock (1963), Feduccia (1980), Cracraft (1981), Elzanowski (1981), Martin (1983*b*, 1984), and Thulborn (1984), and references cited therein. Aves is diagnosed within ornithurine birds by the possession of the following synapomorphies: loss of teeth on maxilla and dentary, well-developed bill; parietals confined to posteriormost portion of skull roof; loss of coronoid bone; presence of bony mandibular symphysis; presence of tricondylar articulation between quadrate and mandible; narrow, fingerlike odontoid process of axis; saddle-shaped intervertebral articulations fully developed and extend into posterior trunk vertebrae (convergent within Hesperornithes); free portion of tail composed of fewer than nine vertebrae (some *Larus* and penguins display varying degrees of fusion of the first caudal, but the nine caudals so obtained are considered reversals); large, dorsally oriented, plowshare-shaped pygostyle that forms a single element in adults (pygostyle absent in some tinamous and neognaths, and in most ratites); fused uncinate processes (reversed in loons, grebes, penguins, and *Apteryx*, and occasionally unfused in other ratites); glenoid surface not perpendicular to external surface of scapula; single prominent articular surface of humerus separated from external tuberosity; pneumatic skeleton, including fossa and foramen in humerus (reversed in some diving birds; S. Hope, pers. comm.); ulnar crest not in plane of long axis of humeral head; presence of lateral extension of internal tuberosity of humerus (=crus laterale tuberculi medialis); deltopectoral crest of humerus with palmar deflection, and apex not distally placed, so distal profile does not curve abruptly to shaft at a steep angle; ilium further lengthened anteriorly so that it overlaps bases of at least one set of ribs; process on proximal portion of ischium contacts pubis; pubis thin; tibia with ossified supratendinal bridge in adult (reversed in some ratites and owls); hypotarsus forms as outgrowth of distal tarsal cap; small foramina pierce tarsometatarsus proximally; fully enclosed foramen between distal ends of metatarsals III and IV for passage of M. extensor brevis digiti IV (this foramen is incompletely enclosed in *Ichthyornis*, and the degree of enclosure may be variable in some ratites).

Numerous characters from less preservable portions of the anatomy, together with ethologic, physiologic, genetic, and immunological data attesting to the distinctiveness of Aves within extant Amniota could be cited at this point. However, because no one has ever mistakenly placed an extant bird in any other extant amniote group aside from Aves, there is little to be gained from belaboring the issue.

Phylogenetic Analysis

I. Phylogenetic Relationships within Dinosauria

In order to address the question of the phylogenetic relationships among the basic taxa, it is first necessary to develop a more inclusive hypothesis that would provide a relevant series of outgroups. Based on evidence presented in Appendix A, Dinosauria is considered monophyletic. Moreover, Herrerasauridae* is considered the sister-group(s) of all other dinosaurs, and Pterosauria-*Lagosuchus*, Ornithosuchidae, *Euparkeria**, and Pseudosuchia represent successively more remote outgroups of Dinosauria.

In view of the ample evidence supporting the hypotheses that Theropoda (see below), Ornithischia, and Sauropodomorpha (including "prosauropods") are each monophyletic (see Appendix A), none of these taxa could have "given rise" to the others. Accordingly, Bakker and Galton's (1974) suggestion that some dinosaurs evolved from "prosauropods" must be rejected (see Charig 1976*b*, for criticisms; see Bonaparte 1976, and Cooper 1981a, for more recent restatements of the "prosauropod" origins hypothesis). Instead, "prosauropods" are considered paraphyletic because some are closer to sauropods than others (Appendix A). Given the monophyly of Theropoda, Sauropodomorpha, and Ornithischia, there are only three phylogenetic relationships possible among these taxa: 1) Ornithischia could be the sister-group of Theropoda; 2) Ornithischia could be the sister-group of Sauropodomorpha; or 3) Sauropodomorpha could be the sister-group of Theropoda. The evidence supporting each of these alternatives will be considered below.

Hypothesis I: Two apomorphies are shared by Theropoda and Ornithischia that are not also present in Sauropodomorpha ancestrally. Ancestral Dinosauria possessed three sacral vertebrae, ancestral Sauropodomorpha retained this condition although subgroups within this taxon have as many as six sacral vertebrae (Appendix A). In contrast, Theropoda and Ornithischia have more than three sacrals; at least five are present in Theropoda ancestrally, and the lowest number reported in Ornithischia is the four in the "juvenile" *Scelidosaurus* (given the sexual dimorphism in ornithischian sacral number, the count should be four to five for ornithischians ancestrally; see Galton 1974, 1982).

Reduction of the fifth pedal digit to a metatarsal spur is another apomorphic condition that is shared by Ornithischia and Theropoda, because the fifth digit retains a single phalanx in Sauropodomorpha ancestrally.

Hypothesis II: Cooper (1981*a*:819–829) reviewed the "prosauropod" characters of ornithischians. Except for the structure of the iliac prong and cheek teeth, the characters he discussed are uniformly ancestral conditions at this level of analysis (i.e., they apply to the immediate common ancestor of Dinosauria). Bakker and Galton (1974) suggested that the elongate anterior process of the ilium (=iliac prong) present in two sauropodo-

morphs, *Anchisaurus* and *Ammosaurus,* indicated a more recent common ancestry between Sauropodomorpha and Ornithischia, in that the iliac prong in the latter group is relatively longer than in other archosaurs. Cooper (1981*a*, fig. 39) noted that the iliac prong may lengthen during ontogeny in *Massospondylus,* but not to the degree seen in either *Anchisaurus* or *Ammosaurus* (see Galton and Cluver 1976). Because the anterior iliac process is comparatively short in all other Sauropodomorpha, including the morphologically generalized members of this group such as *Thecodontosaurus**, this synapomorphy is diagnostic of *Anchisaurus* and *Ammosaurus* alone among Sauropodomorpha. Cooper (1981*a*) considered *Anchisaurus* to be a juvenile *Ammosaurus.* However, neither taxon displays the characteristic skeletal fusions indicating cessation of growth, so Cooper's hypothesis cannot yet be evaluated. Moreover, Galton (pers. comm.) doubts Cooper's ontogenetic argument because these taxa differ not only in size but in the morphology of the ischium, pubis, pes, and third sacral rib. In any case, this apomorphy cannot be considered evidence supporting sauropodomorph-ornithischian monophyly.

Closely packed, leaf-shaped cheek teeth are apomorphic for archosaurs. Analogous tooth-forms reflect herbivorous habits in extant lepidosaurs. Relatively widely spaced, sharply pointed teeth with finely serrated margins are the ancestral condition for archosaurs (Romer 1956). In sauropodomorphs and ornithischians ancestrally, however, the cheek teeth differ in that the compressed crowns are distinctly set off from the root, the teeth are more closely spaced, and there are fewer and larger serrations on the margins of the crowns than in archosaurs ancestrally. The cheek teeth differ in the two groups: in sauropodomorphs the crowns are elongate, and the serrations are finer and more numerous than in ornithischians; but in ornithischians the crowns are nearly as wide as tall, and the serrations are fewer and larger than in sauropodomorphs. Charig (1967*b*) argued that these differences preclude derivation of one tooth-form from the other, and that it was equally likely that both were derived from the more general condition retained by theropods ancestrally. In the absence of pertinent developmental information, Charig's first assertion is not testable. One must admit that the second assertion is possible, but fewer assumptions are involved in accepting that the apomorphic aspects of tooth-form shared by Ornithischia and Sauropodomorpha constitute a potential synapomorphy.

Hypothesis III: Hypotheses of theropod-ornithischian monophyly or ornithischian-sauropodomorph monophyly are each supported by only one or two potential synapomorphies. Thus, there is little basis for preferring one of these alternatives over the other. However, neither hypothesis fares well against the final alternative, the taxon composed of sauropodomorphs and theropods, the Saurischia.

Because Sauropodomorpha and Theropoda are likely to be plesiomorphic with respect to synapomorphies diagnostic of Ornithischia, we have from Seeley (1887, 1888) to the present day considered "saurischians" to be "primitive dinosaurs" (hence Galton's 1977 description of *Herrerasaurus** as a "primitive saurischian," even though it was described as being "primitive" compared to all other dinosaurs). In light of evidence presented below, it will be apparent that "saurischians" are not the paraphyletic "stem-group" of other dinosaurs. Indeed the lineage of dinosaurs of which extant birds are a part, the Saurischia, is the monophyletic sister-taxon of Ornithischia within Dinosauria.

Saurischia

(n. comb.=Saurischia Seeley, 1887, plus Aves Linne, 1758)

Temporal Range.—late Triassic to Recent.
Included Taxa.—Sauropodomorpha and Theropoda (including birds).

Diagnosis.—Saurischia is here defined to include birds and all dinosaurs that are closer to birds than they are to Ornithischia. In the ensuing analysis, Herrerasauridae*, Pterosauria-*Lagosuchus,* Ornithosuchidae, *Euparkeria**, and Pseudosuchia will be used as successively more remote outgroups. Saurischia possesses the following synapomorphies distinguishing it within Dinosauria.

1) Contact between maxillary process of premaxilla and nasal reduced or absent. The maxillary process of the premaxilla is broadly in contact with the nasal at the posterodorsal end of the lateral margin of the external naris in archosaurs ancestrally (Benton 1983; Gauthier 1984). This condition is also ancestral for dinosaurs because it is retained by all Pseudosuchia except some aetosaurs (Sawin 1947), and it is retained by *Euparkeria** (Fig. 1A), Ornithosuchidae (Fig. 1B), and Herrerasauridae* (D. Brinkman, pers. comm.). Compared to the ancestral condition, Ornithischia is further derived in the pronounced posterior extension of the premaxilla (Fig. 1C, D), which may completely separate the maxilla from the nasal in some ornithischians (Romer 1956). Rauisuchia is also diagnosed among Pseudosuchia by a long, but very thin, maxillary process of the premaxilla, and it is thus convergent on Ornithischia in this regard (Gauthier 1984). In contrast to the ancestral condition in Dinosauria, the maxillary process of the premaxilla is reduced and its contact with the nasal is either narrow or absent in Sauropodomorpha (Fig. 1E, F), Ceratosauria (Welles 1984), Carnosauria (Fig. 1G, H), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 1J, K), and birds (Fig. 1L). Ornithomimidae (Fig. 1I) is an exception among Saurischia, in that it displays a prominent maxillary process of the premaxilla. In the context of the evidence presented below, however, ornithomimids are considered to have reversed this character. In all birds except *Archaeopteryx**, the maxilla is also excluded from the external naris. This is not the ancestral condition, however, in that exclusion is effected by an elongate descending process of the nasal, rather than an ascending process of the premaxilla (Marsh 1880; Gingerich 1976). Pterosauria also has a reduced maxillary process (Wellnhofer 1978), and in this detail of premaxillary form pterosaurs are considered convergent with Saurischia.

2) Temporal musculature extends onto frontal. The temporal musculature originates on the dorsolateral surface of the parietal in saurians ancestrally (Gauthier 1984). During postnatal ontogeny, the temporal musculature hypertrophies and its area of origin extends medially onto the parietal table (Gauthier et al., in press). This condition is retained by Pseudosuchia (Gauthier 1984), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), and Ornithischia (Galton 1974), so it appears to be ancestral for Dinosauria as well. In contrast, the temporal musculature extends onto the posterodorsal surface of the frontal bone in Sauropodomorpha (e.g., Huene 1906, 1908, 1932), *Procompsognathus** (Fraas 1913), Ceratosauria (T. Rowe, pers. comm.; Gilmore 1920), Carnosauria (Madsen 1976), *Saurornitholestes** (Sues 1978), Caenagnathidae (Barsbold 1983), Ornithomimidae (Osmolska et al. 1972), and Deinonychosauria (Colbert and Russell 1969). This character has not been reported

in any bird. In view of the evidence presented below, however, it is simpler to accept that the failure of the temporal musculature to reach the frontal results from expansion of the braincase in birds, rather than retention of an ancestral condition.

3) Posterior cervicals elongate. Except among the long-necked protorosaurs, the neck constitutes approximately 33% of the total length of the presacral vertebral column in nonarchosaur Archosauromorpha (Gauthier 1984). There are relatively few complete and articulated vertebral columns known for basal dinosaurian taxa, and comparisons may be complicated by differing numbers of cervical, trunk, and sacral vertebrae, but the available evidence suggests that the neck constituted approximately 40% of the presacral vertebral column in the common ancestor of Saurischia. For example, dividing the combined lengths of vertebrae 2–9 by the combined lengths of vertebrae 2–23 reveals that the neck constitutes 33–34% of the total length in crocodiles (pers. obs.), 34% in *Heterodontosaurus* (Santa Luca 1980), and 33% in *Hypsilophodon** (Galton 1974). In contrast, vertebrae 2–9 constitute 40% of the total length of 2–23 in *Coelophysis* (pers. obs.), 38% in *Compsognathus* (Ostrom 1978), 41%–43% in *Archaeopteryx** (Wellnhofer 1974), and 41% in *Gallimimus* (Osmolska et al. 1972). As has been noted by Galton (1976) and Galton and Cluver (1976), the neck is at least 41% in Sauropodomorpha, not only because of the length of the individual cervicals, but because at least one additional vertebra has been added to the cervical series (see Appendix A). The elongation of the neck appears to have been accomplished by lengthening of the posterior cervicals in Saurischia. Leaving aside the length of the axis, it is evident that vertebrae 3, 4, and 5 are the longest elements in the neck in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975*a*), *Lagosuchus** (Bonaparte 1975*b*), and Pterosauria ancestrally (the neck becomes long within Pterosauria but the neck is short in *Scleromochlus**, the sister-taxon of all other pterosaurs [Gauthier 1984]). This condition is ancestral for Dinosauria in that cervicals 3–5 are also longest in Herrerasauridae* (Galton 1977) and Ornithischia (Galton 1974, 1975, 1978; Santa Luca 1980; Colbert 1981). In contrast, the longest (postaxial) cervicals in saurischians are 6–9. For example, vertebrae 6 and 12 are subequal in length in crocodiles (pers. obs.) and such ornithischians as *Heterodontosaurus* (Santa Luca 1980) and *Hypsilophodon** (Galton 1974). In contrast, cervical 6 is 22% longer than cervical 12 in *Dilophosaurus* (Welles 1984), 37% in *Coelophysis* (pers. obs.), 35% in *Compsognathus* (Ostrom 1978), 62% in *Gallimimus* (Osmolska et al. 1972), and 45% in *Archaeopteryx** (Wellnhofer 1974). Sauropodomorphs also share the apomorphic proportional difference between the lengths of vertebral centra 6 and 12 (e.g., Galton and Cluver 1976). Although our knowledge is less than complete, it appears that elongation of the cervicals posterior to cervical 5 accounts for the neck forming more than 33% of the length of the presacral vertebral column in Sauropodomorpha and Theropoda aside from taxa with large leads and consequently short necks, such as *Tyrannosaurus* (Charig et al. 1965).

4) Axial postzygapophyses set lateral to prezygapophyses. In anterior view, the pre- and post-zygapophyses are approximately equidistant from the midline of the axial centrum in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), *Lagosuchus** (Bonaparte 1975*b*), and Pterosauria ancestrally (Wellnhofer 1975). This condition appears to be ancestral for Dinosauria in that it is retained in Ornithischia (e.g., Ostrom and McIntosh 1966; Ostrom 1970). In contrast, the prezygapophyses lie closer to the midline so that the postzygapophyses are entirely lateral to the prezygapophyses in anterior view in Sauropodomorpha (Fig. 3D), Ceratosauria (Fig. 3E), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and Avialae (Fig. 3G).

5) Epipophysis present on anterior cervical postzygapophyses. Epipophyses (=processus dorsalis of Boas 1929, or anapophysis of Zusi and Storer 1969) on the anterior cervical vertebrae are absent in Pseudosuchia (pers. obs.), *Euparkeria* (Ewer 1965), Ornithosuchidae (Bonaparte 1975*a*), and *Lagosuchus* (Bonaparte 1975*b*), although they may be present at the base of the neck in fully adult archosaurs such as *Alligator* (pers. obs.). Epipophyses are also absent in Pterosauria ancestrally although they are present in Pteranodontidae (Wellnhofer 1978). The anterior cervicals lack epipophyses in Dinosauria ancestrally because these processes are absent in Herrerasauridae* (Galton 1977) and Ornithischia (e.g., Santa Luca 1980). In contrast to the ancestral condition in Dinosauria, epipophyses are present in Sauropodomorpha (Fig. 3D; and see Hatcher 1901, 1903; Huene 1908), Ceratosauria (Fig. 3E; and see Welles 1984), Carnosauria (Osborn 1917), *Compsognathus* (pers. obs.), *Coelurus** (Marsh 1881*a*, 1884*a*), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and birds (Fig. 3G). Epipophyses are present on at least the second through the fourth cervicals, with those on the axis being the most prominent; less prominent epipophyses may be present throughout the cervical series in large theropods (e.g., *Allosaurus;* Madsen 1976). Epipophyses extend caudally and somewhat laterally from the dorsal surfaces of the cervical postzygapophyses; they are largest anteriorly and diminish in size posteriorly. In birds they are associated with the insertions and origins of a variety of dorsal cervical muscles, such as the M. spleni colli, M. spinalis cervicis, M. ascendentes cervicis, and M. intercristales. Some muscles insert directly onto the epipophyses, and others indirectly through insertion on an aponeurosis extending back from the epipophysis (Zusi and Storer 1969). The crocodilian homologues of these muscles have yet to be determined.

6) Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae. Accessory intervertebral articulations are absent in all Pseudosuchia except some Rauisuchia (Charig 1976*b;* Bonaparte 1981) and Aetosauria (M. Parrish, pers. comm.); such articulations are also absent in *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte, pers. comm.), *Lagosuchus** (Bonaparte 1975*b*), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Galton 1977), and Ornithischia (Steel 1969). Thus, accessory intervertebral articulations are absent in Dinosauria ancestrally. As noted most recently by Steel (1970) and Bakker and Galton (1974), Theropoda and Sauropodomorpha alone among dinosaurs possess hyposphene-hypantra accessory intervertebral articulations in the trunk region. Hyposphene-hypantra articulations are present in Sauropodomorpha (e.g., Cooper 1981*a*), *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976), *Coelurus** (Marsh 1884*a*), *Microvenator** (Ostrom 1970), Ornithomimidae (Osmolska et al. 1972), and Deinonychosauria (Ostrom 1969*b*). The vertebrae of *Archaeopteryx** are not exposed appropriately

to determine if hyposphene-hypantra accessory intervertebral articulations are present, but other birds do not possess hyposphene-hypantra. The vertebrae of birds are highly modified, however, and in the context of all the evidence it is simpler to accept that their intervertebral articulations are further modifications of the saurischian condition, not the retention of an ancestral intervertebral articulation.

7) Manus more than 45% of length of humerus plus radius. The longest digit in the manus (plus its metacarpal) is 28% of the length of the humerus plus radius in the early crocodile *Protosuchus* (Colbert and Mook 1951); this length is proportionately longer in extant crocodiles displaying negative allometry in limb length (e.g., 37% in *Crocodylus porosus* and *Caiman sclerops*, pers. obs.). These size relationships appear to be ancestral for dinosaurs because in ornithischians such as *Scutellosaurus** (38%; Colbert 1981), *Lesothosaurus* (26–29%; estimates based on Galton 1978), and *Hypsilophodon* (34%; Galton 1974), the longest manal digit and its metacarpal is no more than 38% of the length of the humerus plus radius. The single exception appears to be *Heterodontosaurus*, in which the manus is 56% of the length of the humerus plus radius. This attribute is considered diagnostic of this taxon among Ornithischia (Santa Luca 1980). In contrast, the longest digit and its metacarpal is at least 45% of the length of the humerus plus radius in Saurischia ancestrally. For example, the manus is 45% to 47% of the length of the humerus plus radius in *Thecodontosaurus**, 60% in *Efraasia** (estimates based on Huene 1914*c* and Galton 1973*a*), 47% in *Syntarsus* (Raath 1969) and *Coelophysis* (Ostrom 1969*b*), 77% in *Allosaurus*, 75% in *Deinonychus*, and 58% in *Ornithomimus* (Ostrom 1969*b*).

8) Manus markedly asymmetrical. In archosaurs ancestrally, the inner digits of the manus are stouter than are the outer digits, and the third digit is the longest digit in the manus (Fig. 4G). The asymmetry of the manus becomes more pronounced within ornithosuchian archosaurs and yields a further reduction of the outer two digits of the manus in dinosaurs ancestrally (Fig. 4H–O). Pterosaurs are exceptional among Archosauria: the enormously enlarged fourth digit supporting the wing membrane can hardly be considered the ancestral condition for archosaurs, and the hand is not modified this way in *Scleromochlus* (Huene 1914*a*). Nevertheless, the pterosaur's third digit is the longest of the digits remaining unmodified. Ornithischia retains the ancestral condition: digit three is longest (Fig. 4H). In contrast to the ancestral condition in dinosaurs, however, the inner two digits (two and three) of the manus are further enlarged, so that the second, rather than the third, is now the longest digit in the hand in Sauropodomorpha (Fig. 4I, J), Ceratosauria (Fig. 4K), Carnosauria (Fig. 4L), *Ornitholestes** (Osborn 1917), Elmisauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). Asymmetrically developed hands are characteristic of Archosauria, and this modification becomes more pronounced within Ornithosuchia, culminating in the markedly asymmetrical hands of birds. To be complete, a process-related theory of limb development must account for this peculiarity; likewise, one must be cautious in developing a general theory of hand morphogenesis based largely or exclusively on the hands of extant birds.

9) Bases of metacarpals IV and V lie on palmar surfaces of manal digits three and four respectively. The ancestral condition in Sauria (=extant diapsids; Gauthier 1984) is that the bases of the medial metacarpals overlap the bases of the lateral metacarpals. This condition is retained by Pseudosuchia (Fig. 4G), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), and Ornithischia (Fig. 4H). Unlike other archosaurs, however, the base of metacarpal IV, and to a greater extent that of V, lie more on the palmar surface of the hand in Sauropodomorpha (e.g., Janensch 1922; Cooper 1981*a*:740, fig. 37, 38). The base of the fourth digit of early theropods such as Ceratosauria also lies on the palmar surface of the base of the third digit (e.g., Welles 1984:153, fig. 37; I thank T. Rowe for pointing out that the sauropodomorph condition also applies to theropods). The fifth manal digit is absent from the ontogeny of extant Theropoda; however, Colbert's unpublished drawing of an intact hand of *Coelophysis* reveals a nubbin of bone lying on the palmar surface of the base of metacarpal IV. Because this piece of bone lies in the same position as the fifth digit in sauropodomorphs, Colbert's interpretation of this element as a remnant of the fifth digit is probably correct. In more derived Theropoda the fourth manal digit is lost, although it is retained in embryos of extant birds, and a small remnant of this digit has been observed on the palmar surface of the hand in *Ornitholestes** (Osborn 1917; see Part III, character 45 for further discussion).

10) Saurischian pollex. In Archosauria ancestrally, metacarpal I is only a little shorter than II, phalanx I of the first digit is shorter than metacarpal I, and the claw-bearing ungual is neither very large nor sharply pointed (Gauthier 1984). This condition is retained in Pseudosuchia (Fig. 4G). Aside from the offset head of metacarpal I and a relatively larger and more sharply pointed ungual, the first digit and its metacarpal in Ornithosuchidae (Bonaparte 1975*a*) and Ornithischia (Fig. 4H) is as in archosaurs ancestrally. Manal digit one, the pollex, of Theropoda and Sauropodomorpha differs from that of other Archosauria in several ways. First, the pollex is more robust and bears a larger ungual phalanx (Fig. 4I–O); this character is extreme within Sauropodomorpha (Fig. 4I, J). Second, metacarpal I is only half or less the length of metacarpal II, and the distal condyles are more markedly asymmetrical (Fig. 4I, K; see Welles 1984). Third, the first phalanx is much longer than metacarpal I; the first phalanx equals or exceeds the length of any other phalanx in the hand (Fig. 4I–O). Galton (1971), Bakker and Galton (1974), and Baird (1980) discussed the grasping ability of dinosaur hands, and commented on the range of motion possible in the saurischian pollex, noting that the articular surfaces allow a fairly precise reconstruction of the range of possible movements. Galton (1971) described how the articular surfaces within the saurischian pollex force the claw to diverge and point inward during extension and to converge with the second and third digits and point downwards during flexion; at maximum extension the claw points inward to a greater degree in Sauropodomorpha than in Theropoda. As *Massospondylus* indicates (Fig. 4J), the manus was modified to play a greater role in support and locomotion early in sauropodomorph history; the entire hand became broader, shorter, and more robust, and the first phalanx and metacarpal were likewise shortened. Aside from the large claw, scarcely any evidence of the grasping hand of saurischians remains in the elephantine hands of Sauropoda (e.g., Janensch 1922). Although

the first digit is seldom used for grasping in ornithurine birds, its functional independence has been conserved. Indeed, the dinosaurian modifications of the first digit toward the alula, appears to have been essential to the development of powered flight in birds (Bellairs and Jenkin 1960).

Saurischian monophyly is supported by shared apomorphies in construction of the snout, pattern of hypertrophy of the temporal musculature, elongation of the cervical region, modification of the axial zygapophyses, presence of epipophyses in the anterior cervicals, accessory intervertebral joints, and a variety of distinctly avian modifications of the manus. Possible alternative hypotheses are less able to account for observed patterns of shared apomorphies; accordingly, Sauropodomorpha and Theropoda (including birds) are hypothesized to be sister-groups within Saurischia, and Ornithischia is considered to be the sister-group of Saurischia within Dinosauria.

II. Phylogenetic Relationships within Theropoda

Theropoda

(n. comb.="Theropoda" Marsh, 1881*b*, plus Aves Linne, 1758)

Temporal Range.—late Triassic to Recent.

Included taxa.—*Procompsognathus**, *Lilienstermus**, Ceratosauria, Carnosauria, Ornithomimidae, *Compsognathus*, Caenagnathidae, Elmisauridae*, *Microvenator**, *Coelurus**, *Saurornitholestes**, *Hulsanpes*, *Ornitholestes**, Deinonychosauria, and Avialae. The reader is referred to Olshevsky (1978) and Welles (1984) for additional nonavian theropod taxa that were not considered in this investigation.

Diagnosis.—Theropoda is defined ostensively to include birds and all saurischians that are closer to birds than they are to sauropodomorphs. Sauropodomorpha, Ornithischia, Herrerasauridae*, Pterosauria-*Lagosuchus*, Ornithosuchidae, *Euparkeria**, and Pseudosuchia will be used as successively more remote outgroups in the following analysis. Theropods are distinguished from other saurischians by the following synapomorphies.

11) Reduced overlap of dentary onto postdentary bones and reduced mandibular symphysis. Many extant birds display some degree of intramandibular mobility, and several authors have noted that the construction of nonavian theropod mandibles also allows intramandibular mobility (e.g., Gingerich 1976). Extant Pseudosuchia have solidly constructed mandibles that show no indication of intramandibular mobility. That is to say, crocodilians display a broad overlap between dentary and postdentary bones (with the dentary extending to the level of the orbit), a process of the dentary passing dorsal to the mandibular fenestra, and a prominent mandibular symphysis. Each of these attributes indicates the absence of intramandibular mobility, and they are retained in nontheropod ornithosuchians, including Ornithischia (Fig. 1C, D; Romer 1956) and Sauropodomorpha (Fig. 1E, F; Galton 1984). In contrast, the mandibular symphysis is reduced in Theropoda and the overlap of the dentary onto the postdentary bones is very reduced, such that the anterodorsally sloping posterolateral margin of the dentary terminates antorbitally (Fig. 1G–L). This region of the mandible is poorly preserved in *Archaeopteryx**, but Gregory (1952) described the similarities between the intramandibular joints of *Ichthyornis* and Hesperornithes and those of some squamates with intramandibular kinesis. Many extant lineages of Aves retain the ancestral relations of theropod dentary and postdentary elements and intramandibular mobility (e.g., *Larus*). However, birds with noncarnivorous diets, and short and stout jaws with broad mandibular symphyses, do not.

12) Lacrimal broadly exposed on skull roof. The lacrimal forms the posterodorsal and posterior margins of the antorbital fenestra, but does not participate in the formation of the skull roof in Pseudosuchia (Bonaparte 1981), *Euparkeria** (Fig. 1A), Ornithosuchidae (the lacrimal gains some exposure dorsally as part of the supraorbital cornice; Fig. 1B), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 1C, D), and Sauropodomorpha (Fig. 1F). In contrast to the ancestral condition, the lacrimal forms much of the skull roof anterior and lateral to the prefrontal above the orbit in *Procompsognathus** (pers. obs.), Ceratosauria (Welles 1984), Carnosauria (Fig. 1G, H), Ornithomimidae (Fig. 1I), Deinonychosauria (Fig. 1J, K), *Compsognathus* (pers. obs.), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), and Avialae (Fig. 1L; see Part V, character 67).

13) Presence of maxillary fenestra. An accessory fenestra within the antorbital fossa is absent in all Pseudosuchia (Krebs 1976), *Euparkeria** (Fig. 1A), Ornithosuchidae (Fig. 1B), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 1C, D), and Sauropodomorpha (Fig. 1E, F). Thus, a maxillary fenestra is absent in Saurischia ancestrally. In contrast, a small fenestra lies at the anterior margin of the antorbital fossa in Ceratosauria (T. Rowe, pers. comm.), and a larger fenestra lies in a more posterior position within the antorbital fossa in Carnosauria (Fig. 1G, H), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 1I), Deinonychosauria (Fig. 1J, K), and *Archaeopteryx** (Fig. 1L). This character is absent and has presumably been lost in Ornithurae (see Part III, character 37).

14) Vomers fused anteriorly. The vomers are short, narrow, and paired in Archosauria ancestrally (Gauthier 1984); to judge from the condition seen in Pseudosuchia (aside from the comparatively long vomers of aetosaurs, Walker 1961), *Euparkeria** (Fig. 2A), Ornithosuchidae (Fig. 2B), and Pterosauria (Wellnhofer 1978) this condition appears ancestral for Ornithodira (Appendix A). In contrast, the vomers are elongate, extending well posterior to the level of the anterior limit of the palatine in Ornithischia ancestrally (Galton 1974; Heaton 1972), Sauropodomorpha ancestrally (Huene 1906, 1908, 1932; Galton 1984), and Theropoda aside from Neognathae (pers. obs.), and this appears to be the ancestral condition in Dinosauria. Few nonavian theropod fossils have this region of the skull preserved. Theropoda differs from dinosaurs, other than thyreophoran ornithischians (P. Sereno, pers. comm.), in that the vomers are indistinguishably fused anteriorly (although they may be paired in a few neognaths, pers. obs., and in *Hesperornis*, L. Martin, pers. comm.). Nevertheless, the presence of the apomorphic condition in theropods as diverse as *Procompsognathus** (Ostrom 1981), *Ceratosaurus* (T. Rowe, pers. comm.), *Deinonychus* (Ostrom 1969*b*), *Allosaurus* (Fig. 2C), *Tyrannosaurus* (Fig. 2D), *Oviraptor* (Osmolska 1976), *Gobipteryx* (Elzanowski 1977, 1981), and Ratitae and Tinami (Huxley 1867), suggests that the vomers are fused anteriorly in Theropoda generally. Walker (1964) described the enlarged, diamond-shaped anterior ends of the vomers in *Ornithosuchus* as being similar to the condition of the fused anterior third of the vomer in *Tyrannosaurus*. However, this similarity obtains between *Tyrannosaurus* and *Ornithosuchus* alone. Moreover, the paired and short vomers of the latter (Fig. 2B) are otherwise plesiomorphic

with respect to those of all other theropods, including *Tyrannosaurus* (Fig. 2D).

15) Expanded ectopterygoid with ventral fossa. Colbert and Russell (1969) argued that in early theropods (e.g., Ceratosauria) the ectopterygoid was "simple" and without a ventral fossa. However, I have observed this fossa in the ceratosaur *Coelophysis.* I agree with the observation that there is an expanded ectopterygoid with a more or less prominent fossa ventrally in the main body of the element in Carnosauria, Ornithomimidae, and Deinonychosauria (Colbert and Russell 1969), *Saurornitholestes** (Sues 1978), and in Caenagnathidae (Barsbold 1983). This character cannot be determined in *Archaeopteryx**, and the ectopterygoid has not been identified with certainty in Ornithurae (see McDowell 1978). In the context of all the evidence, birds are considered to have attained their current condition from an ectopterygoid like that seen in theropods generally.

16) First intercentrum with large occipital fossa and small odontoid notch. The occipital fossa on the anterior face of the first intercentrum is more than three times as wide as it is tall and the odontoid notch is consequently broad and deep in Pseudosuchia (pers. obs.), *Euparkeria** (Ewer 1965), Ornithischia (Fig. 3A), and Sauropodomorpha (Hatcher 1901). In contrast, the occipital fossa is only about twice as wide as it is tall and the odontoid notch is consequently smaller in Ceratosauria (Fig. 3B), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Ostrom 1969*b*), and Avialae (Fig. 3C).

17) Second intercentrum with broad, crescentic fossa anteriorly for reception of first intercentrum. The articular surface on the anteroventral margin of the axial (2nd) intercentrum is convex in Pseudosuchia (pers. obs.). Dinosaurs differ from the ancestral condition in Archosauria in that this articular surface is at least partly concave (Fig. 3D). Compared to other dinosaurs, however, the articular surface on the axis for the first intercentrum forms a broad, deep, and concave fossa in Ceratosauria (Fig. 3E), Carnosauria (Gilmore 1920), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F), and Avialae (Fig. 3G).

18) Pleurocoelous presacral vertebrae, particularly in cervical region. Fenestra leading into hollow centra (=pleurocoels) are absent in Pseudosuchia (Romer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Walker 1964), *Lagosuchus** (Bonaparte 1975*b*), Herrerasauridae (Galton 1977), Ornithischia (Romer 1956), and Sauropodomorpha ancestrally (Cooper 1981*a*). Thus, nonpleurocoelous vertebrae are the ancestral condition for Saurischia. In contrast, pleurocoels are present in all Theropoda; Ostrom (1978) discussed the distribution of this character within the group, noting regional variations in the presacral column. Pleurocoels are present in Ceratosauria (Gilmore 1920), Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), *Saurornitholestes** (Sues 1978), *Coelurus** (Marsh 1884*a*), *Microvenator** (Ostrom 1970), Deinonychosauria (Ostrom 1969*b*), and Avialae (Ostrom 1976*a*). Analogous modifications are known in Pterosauria (Wellnhofer 1978) and Sauropoda (Marsh 1896), but this is considered convergence because pleurocoels are absent in their respective outgroups among sauropodomorphs, ornithischians, herrerasaurs*, and *Lagosuchus**.

19) At least two additional vertebrae incorporated into sacrum (including at least one from the caudal series and at least one from the trunk). As argued above, three sacrals are present in Dinosauria ancestrally. In contrast, no theropod in which the sacrum is coossified and intact has fewer than five sacrals. Among theropods, the character has been reported in Ceratosauria (Raath 1969), Carnosauria (Steel 1970; Madsen 1976), Ornithomimidae (Osborn 1917), Deinonychosauria (Barsbold 1974), and Avialae (Ostrom 1976*a*). Ornithurae has many more vertebrae in the sacrum, a character that is by no means unique to Theropoda. As noted above, a sacrum consisting of at least four to five vertebrae may also be ancestral for Ornithischia. The *Heterodontosaurus* (Santa Luca 1980) and ornithopod (Galton and Jensen 1973) lineage of Sereno (1984) has at least five or six, which is also the lowest number reported in pachycephalosaurs and ceratopsians, with the latter group possessing as many as eleven sacrals (Steel 1969). In addition, subgroups within Pterosauria (Wellnhofer 1978) and Sauropoda (Berman and McIntosh 1978) have five or more sacrals.

20) Transition point in tail (sensu Russell 1972). In Dinosauria ancestrally, the caudal zygapophyses are short and vertically oriented, and the transverse processes are present posterior to the middle of the caudal series (Santa Luca 1980; Cooper 1981*a*). In contrast to the condition retained by Sauropodomorpha, however, in Theropoda the neural arches and the transverse processes are reduced posteriorly so that they are absent in most of the posterior half of the tail. In addition, the caudal prezygapophyses in the posterior half of the tail are elongate, pointed anteriorly, and clasp the elongate, blocklike postzygapophysial moiety. Finally, the caudal haemal arches in at least the posterior third of the tail are depressed and boat-shaped in lateral outline (e.g., Fig. 3E, F). The degree of transformation in each of these aspects of caudal morphology is not precisely correlated. Although the zygopophyses may begin elongation prior to complete loss of transverse processes, with modified haemal arches subsequently appearing further posteriorly, these transformations take place within a few vertebrae of one another; accordingly, they are described collectively as the "transition point." The least-modified tails seen among theropods are present in Ceratosauria (Raath 1969). However, the transformation in caudal form is more profound and the transition point begins closer to the base of the tail in Carnosauria (Lambe 1917), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), Ornithomimidae (Osmolska et al. 1972), Caenagnathidae (Barsbold 1983), Deinonychosauria (Ostrom 1969*b*), and *Archaeopteryx** (see Part III, character 40). The tail is further modified in Ornithurae, in that the proximal caudal zygapophyses are lost, but the tail still retains mobile proximal and stiff distal portions (i.e., the pygostyle). Moreover, in Hesperornithes that possess a multisegmented pygostyle in the adult, these caudal vertebrae have lost the neural spines and transverse processes. Although lacking the ventral keel, boat-shaped haemal arches are retained in the proximal caudals in Hesperornithes (L. Martin, pers. comm.) and in several other ornithurine birds, such as *Ichthyornis,* penguins, and loons (Marsh 1880). A similarly stiffened posterior part of the tail arose convergently in *Staurikosaurus** (Galton 1977); and vaguely similar modifications are present in ankylosaurs, in which the distal extremity of the tail bears a club (Coombs 1978*a*). An analogous condition, although highly modified in a fashion similar to dromaeosaurs, arose convergently within Pterosauria (i.e., the tail in *Scleromochlus** is not stiffened). The tail of *Staurikosaurus** could be construed as evidence of a relationship to theropods. How-

ever, so far as *Staurikosaurus** is preserved, it lacks the diagnostic characters of Saurischia, and it shares an expanded distal end of the pubis with *Herrerasaurus** (Galton 1977; and see Gauthier 1984).

21) Enlarged distal carpal I overlaps bases of metacarpals I and II. Few early archosaurs have well-preserved hands, but aetosaur (Sawin 1947) and embryo crocodilian pseudosuchians (pers. obs.) are like Ornithischia (e.g., Fig. 4H) in retaining the ancestral saurian condition, in which the distal carpals are restricted to the bases of their respective metacarpals. This region is not preserved in *Efraasia**. In *Thecodontosaurus** distal carpal I is also confined to the base of metacarpal I, but the base of metacarpal II and its associated distal carpal are not preserved (Huene 1914*c*). The only reasonably complete hands of early sauropodomorphs are those of *Massospondylus* and some plateosaurs (e.g., Huene 1932; Young 1941, 1947, 1958; Galton and Cluver 1976:135, fig. 7). Based on published illustrations, personal communications from P. Galton, and personal observation of *Plateosaurus*, it appears that distal carpal I is restricted to the base of metacarpal I in Sauropodomorpha ancestrally. *Massospondylus* may be an exception, in that distal carpal I overlaps distal carpal II, although the former is separated from metacarpal II by the latter (Fig. 4J; and see Cooper 1981*a*:737, fig. 32). In contrast, *Halticosaurus** (Huene 1934), Ceratosauria (Fig. 4K), Carnosauria (Fig. 4L), *Coelurus** (Ostrom 1976*a*), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O) are distinguished from other archosaurs in that an enlarged distal carpal I overlaps the bases of the inner two metacarpals, thus functionally integrating digits I and II in the wrist, just as in extant birds. In theropods in which distal carpals I and II are present, a small distal carpal II lies distal and largely posterolateral to distal carpal I; thus distal carpal II lies at least partly between distal carpal I and metacarpal II (Madsen 1976). Distal carpals I and II are fused in *Syntarsus rhodesiensis;* the adult status of the type-specimen is indicated by several other fusions in the postcranial skeleton marking the cessation of growth (Raath 1969). According to Madsen (1976), in *Allosaurus fragilis* the larger distal carpal I and the smaller distal carpal II fuse to one another very late in postnatal development. Ornithomimidae is an exception in that its wrist is composed of small and poorly ossified carpals that lack articular facets (Osborn 1917). Ornithomimids are thus like tyrannosaurid carnosaurs (Barsbold 1983) in that the carpals appear to be arrested at a juvenile stage of development. No separate distal carpal II has been reported in any adult deinonychosaur or bird; the elements are said to arise separately in bird embryos (Heilmann 1926), although Hinchliffe and Hecht (1984) have been unable to identify more than a single condensation in *Gallus*.

22) Manal digit V reduced to a vestige or absent. The fifth manal digit is present in all Pseudosuchia (e.g., Fig. 4G), *Euparkeria** (Ewer 1965), and Ornithosuchidae (Bonaparte 1975*a*). And, although the digit is reduced in Dinosauria ancestrally, it is retained by Ornithischia (Fig. 4H) and Sauropodomorpha (Fig. 4I, J). Thus, a fifth manal digit is present in Saurischia ancestrally. In contrast, all that remains of the fifth manal digit in Ceratosauria is the small metacarpal splint lying at the base of the palmar surface of metacarpal IV in *Coelophysis* (Colbert, pers. comm.). No other ceratosaurs are reported to have a vestigial fifth digit, but *Coelophysis* is the only ceratosaur that is well enough preserved to be able to discriminate between absence and nonpreservation. No vestige of the fifth manal digit has been reported in Carnosauria (Fig. 4L), *Compsognathus* (Bidar et al. 1972), *Saurornitholestes** (Sues 1978), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), or Avialae (Fig. 4O). The fifth manal digit is also missing in the ontogeny of extant birds (Heilmann 1926). *Liliensternus** is described as retaining a reduced fifth digit, but Huene's (1934) description and illustration of what remains of the hand speaks against such an interpretation; the metacarpals he interpreted as being III and IV were capped by an enlarged carpal, thus corresponding to metacarpals I and II of other theropods, and there is no evidence of a fifth digit. Loss of the fifth manal digit arose convergently in Pterosauria (Wellnhofer 1978).

23) Manal digit IV reduced or absent in adult. As discussed above, manal digits IV and V are reduced in Dinosauria ancestrally. Theropoda is unique, however, in that manal digit IV is never longer than metacarpal III, and it is never represented by more than a metacarpal with a vestigial phalanx on its distal extremity. Ceratosauria (Fig. 4K) retains the vestigial manal digit IV just described, but the fourth digit is reduced to a mere nubbin of bone or is absent in postembryonic development in Carnosauria (Fig. 4L), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), *Compsognathus* (Bidar et al. 1972), *Saurornitholestes** (Sues 1978), Elmisauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), Deinonychosauria (Fig. 4N), and in all birds beyond embryonic stages (Fig. 4O; Heilmann 1926). The ancestral theropod phalangeal formula is thus 2-3-4-1-0, rather than 2-3-4-3-2 as it is in the hands of Dinosauria and Saurischia ancestrally.

24) Manus with elongate penultimate phalanges. The penultimate phalanges are shorter than the more proximal elements in each digit in Pseudosuchia (Fig. 4G) and Ornithischia (Osborn 1924*a*; *Heterodontosaurus* is apomorphic among ornithischians in this regard, see Fig. 4H). The same can be said for digits two through five in Sauropodomorpha, except that like other saurischians the first metacarpal is relatively short (e.g., Fig. 4J). Thus, a hand with the same internal proportions as archaic sauropodomorphs such as *Thecodontosaurus** (Fig. 4I) appears to be ancestral for Saurischia. Theropods are further derived in that the penultimate phalanges on the functional digits are uniformly longer than the more proximal elements comprising their respective digits. This apomorphy appears in its most general form among Ceratosauria (Fig. 4K), but it is also present in Carnosauria (Fig. 4L); it is further developed in *Saurornitholestes** (Sues 1978), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 4N), and *Archaeopteryx** (Fig. 4O). Ornithurine birds retaining an unmodified first digit usually maintain its ancestral proportions. However, the first phalanx in manal digit II may be subequal to or longer than the second phalanx, and the third digit often retains only one phalanx. The ornithurine carpometacarpus cannot be considered plesiomorphic, and the way in which the ornithurine manus differs from that of other theropods is considered to have arisen secondarily. Pterosaurs also have elongate penultimate phalanges in digits I through III, and this is considered yet another example of convergence between pterosaurs and theropods.

25) Manal digit III with short first and second phalanges. The third phalanx of digit III is shorter than either the first or second in Pseudosuchia (Fig. 4G), Ornithischia (Fig. 4H), and Sauropodomorpha (Fig. 4I, J), so this condition is ancestral for Saurischia. In contrast, the first and second phalanges of manal digit III are short, so that the third phalanx is the longest element in Ceratosauria (Fig. 4K) and Carnosauria (Fig. 4L), and this character is even more markedly developed in Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), *Saurornitholestes** (Sues 1978), and Deinonychosauria (Fig. 4N). This condition is ancestral for Avialae (Fig. 4O), but it is absent in the diagnostically modified carpometacarpus of Ornithurae, in which only one phalanx remains in manal digit III (Heilmann 1926). This character has arisen convergently in Pterosauria, some of which may have very short first and second phalanges as in the subgroup of theropods of which birds are a part (see below), but others may have only the first phalanx shortened (Wellnhofer 1978); the level at which these characters arose within Pterosauria is unknown.

26) Manal unguals enlarged, compressed, sharply pointed, strongly recurved, and with enlarged flexor tubercles. As noted above, modification of the pollex in Ornithosuchidae indicates that the ability to grasp with the hands unites a more inclusive group of Ornithosuchia than Dinosauria alone. Nevertheless, with the possible exception of Pterosauria (Wellnhofer 1978), no archosaurs except theropods have manal unguals so modified as to indicate that they played an important role in securing prey (Ostrom 1969*b*). Impressions of claw sheaths are preserved only in *Compsognathus, Archaeopteryx** (pers. obs.), and *Chirostenotes** (Currie, pers. comm.) among Mesozoic theropods, and claw sheath morphology corroborates estimates of claw-form extrapolated from ungual morphology (Ostrom 1978). Based on ungual morphology, raptorial claws are present in the hands of *Liliensternus** (Huene 1934), Ceratosauria (Gilmore 1920; pers. obs.), Carnosauria (Madsen 1976), *Coelurus** (Ostrom 1976*a*), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), *Saurornitholestes** (Sues 1978), *Microvenator** (Ostrom 1970), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Deinonychosauria (Russell 1969; Ostrom 1969*b*, 1974*b*), and *Archaeopteryx** (Ostrom 1976*a*). The juveniles, and occasionally the adults, of a wide variety of extant birds may retain clawed digits, but with the notable exception of juvenile Hoatzin (*Opisthocomus*) they are virtually nonfunctional in modern birds (Heilmann 1926). As noted above, an enlarged and sharply pointed first ungual is an ancestral condition for Saurischia; however, even this claw only approaches the level of specialization seen in Theropoda (compare *Massospondylus* in Cooper 1981*a*:748, fig. 45, with *Deinonychus* in Ostrom 1969*b*:108, fig. 63). In the context of all the evidence, the hands of Ornithomimidae and Ornithurae are considered secondarily modified in this regard.

27) Preacetabular part of ilium enlarged and extending far forward of acetabulum. A prominent iliac spine arose prior to the origin of Archosauria within Archosauromorpha (Gauthier 1984). The ancestral condition is retained by Pseudosuchia (Romer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975*a*), *Lagosuchus** (Bonaparte 1975*b*), and Sauropodomorpha (Fig. 5B). Ornithischians have a diagnostically elongate iliac spine (Fig. 5A). In contrast, Colbert (1964) noted that an enlarged preacetabular portion of the ilium obtains in all theropods (e.g., Fig. 5C–I). The increased length of the theropod ilium is probably correlated in a general way with the added number of sacrals. The character is not entirely redundant, however, because the addition of sacral vertebrae has not been accompanied by the same modifications of the ilium in other archosaurs. Rowe (pers. comm.) pointed out that the M. puboischiofemoralis internus (2), which originates beneath the posterior transverse processes in crocodiles, has moved onto the enlarged anterior portion of the ilium in Theropoda. Both Walker (1977) and M. Parrish (pers. comm.) believe that this muscle originated from the medial part of the pubis and that the dorsal shift of origin of the pifi 2 (one of the so-called M. iliotrochantericus group found in Aves) to the transverse processes appears to be correlated with reduction of the pubis in crocodilians. Their hypothesis strikes me as *ad hoc,* however, given that this muscle has a dorsal origin, rather than a ventral origin from the pubis, in the only archosaurs in which it can actually be observed.

28) Pronounced brevis fossa. The brevis fossa is a modified area of origin for the M. caudofemoralis brevis on the ventral surface of the postacetabular portion of the ilium (Romer 1923, 1927; Walker 1977). This muscle is largely a retractor of the hindlimb in archosaurs with long ilia (M. Parrish, pers. comm.). Possession of a brevis fossa (or shelf) is an ancestral condition in Dinosauria, although it is also present in cursorial Rauisuchia (Bonaparte, pers. comm.; and see Appendix A). However, the brevis fossa is most markedly developed in Theropoda, in which there is a broad, deep, and elongate fossa on the posteroventral margin of the ilium (see Madsen 1976:145, fig. 46b). The prominent shelf forming part of the brevis fossa often gives the posterior extremity of the iliac blade a squared-off, truncated profile in lateral view (Fig. 5C–E). An enlarged brevis fossa is present in *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976), *Ornitholestes** (Osborn 1917), Ornithomimidae (Osmolska et al. 1972), Elmisauridae* (Currie, pers. comm.), Caenagnathidae (Barsbold 1983), and Deinonychosauria (Ostrom 1969*b*, 1976*a*). The dinosaurian origin of this muscle is retained in birds (Romer 1923), but a brevis fossa as such appears to be absent in Avialae; in light of all the evidence it is simpler to accept reversal rather than plesiomorphy as an explanation for its absence in birds.

29) Femur bowed in a convex arc and sigmoidal curvature less prominent. The femur has a sigmoidal curvature in Archosauria ancestrally (Romer 1956), in that the shaft of the element is S-shaped in two planes (Padian, in press). Dinosaurs retain this condition, because a sigmoidal femur is present in Herrerasauridae* (Galton 1977), and in Ornithischia (Colbert 1981) and Sauropodomorpha ancestrally (Cooper 1981*a*), thus indicating that a sigmoidal femur is the ancestral condition for Saurischia. In contrast, the femur is bowed dorsally and the distal end is inflected laterally so there is little or no sigmoidal curvature in *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Gilmore 1920; Raath 1969), *Coelurus** (Ostrom 1976*a*), *Compsognathus** (Ostrom 1978), *Ornitholestes** (Osborn 1917), *Microvenator** (Ostrom 1970), Ornithomimidae (Osmolska et al. 1972), Elmisauridae* (Currie, pers. comm.), Caenagnathidae (Barsbold 1983), Deinonychosauria (Ostrom 1976*a*), and Avialae (Ostrom 1976*b*). The femur is less bowed in large theropods, especially in Carnosauria, and

Ostrom (1976*b*) suggested that this reflects constraints imposed by large size. The bowed and nonsigmoidal femur arose convergently in Pterosauria (Padian 1983), and it appears to be ancestral for ornithopod ornithischians (Galton and Jensen 1973). This character is evidently related to small size and highly developed cursorial habits in Ornithosuchia (Coombs 1978*b;* Padian 1983).

30) Fibula closely appressed to tibia, and fibula attached to crest on lateral side of proximal end of tibia. The fibula is broadly separated from the tibia for most of its length, and there is no fibular crest on the tibia, in Pseudosuchia (Krebs 1976), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975*a*), and *Lagosuchus* (Bonaparte 1975*b*). This condition is retained in Ornithischia ancestrally (Romer 1956) and in Sauropodomorpha (Cooper 1981*a*). In large dinosaurs, the tibia and fibula are even more broadly separated from one another. However, regardless of size, the fibula is always closely appressed against the lateral face of the tibia in Theropoda. This character is unique to Theropoda among Saurischia (Ostrom 1976*a*), but it arose convergently in Pterosauria (Wellnhofer 1978) and it appears to be the ancestral condition for ornithopod ornithischians (Galton and Jensen 1973). Unlike either of the last mentioned taxa, however, only theropods possess the fibular crest on the tibia. This synapomorphy is present in *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), *Compsognathus* (Ostrom 1978), Carnosauria (Fig. 6A), *Microvenator** (Ostrom 1970), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 6C), Deinonychosauria (Fig. 6B), and Avialae (Bellairs and Jenkin 1960).

31) Metatarsus narrow and elongate. In Ornithodira ancestrally the metatarsus is narrow compared to its length owing to elongation of the metatarsals and reduction of the outer digits (Fig. 6K–P). Within Sauropodomorpha, the manus and pes are shortened, and they are broadened owing to enlargement of digit I (Fig. 6N; this appears to be developmentally correlated with modification of the pollex; Appendix A). In contrast, the theropod metatarsus is relatively long and narrow, and it is thus more like that of birds than is the case in Dinosauria ancestrally (Fig. 6O, P). The only other ornithosuchian with such a narrow and elongate metatarsus is *Lagosuchus** (Fig. 6K). *Lagosuchus** is considered to be convergent with theropods in this regard because the metatarsus is not so narrow in Sauropodomorpha (Fig. 6N), Ornithischia (Fig. 6M), or Herrerasauridae* (Fig. 6L), all of which are closer to Theropoda than is *Lagosuchus**. The proportions of the metatarsus vary with size; the larger dinosaurs possess relatively broad metatarsals compared to related, smaller dinosaurs. This difference appears to reflect scaling effects, and applies to large versus small theropods as well. Nevertheless, according to Ostrom (1976*a*), all theropods have a relatively narrower metatarsus when compared to other dinosaurs of equal size. A narrow, elongate metatarsus has been reported in *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Raath 1969), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Osborn 1917), *Hulsanpes* (Osmolska 1982), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Russell 1969), and Avialae (Ostrom 1976*a*).

32) Pes with pedal digit IV reduced and subequal to II in length, thus making pes symmetrical about digit III. As Ostrom (1981) argued, theropod feet are unlike those of dinosaurs generally; in other dinosaurs pedal digit IV is longer than II (Fig. 6M, N), but in theropods pedal digit IV is reduced and approaches the length of pedal digit II (Fig. 6O), thus making the pes even more symmetrical about digit III than in dinosaurs ancestrally. The symmetrical pes is present in *Procompsognathus** (Ostrom 1981), Ceratosauria (Gilmore 1920; Raath 1969), Carnosauria (Madsen 1976), Elmisauridae* (Sternberg 1932), and Ornithomimidae (Osmolska et al. 1972). In the context of all the evidence, it is more parsimonious to accept that the elongate pedal digit IV of Deinonychosauria (Ostrom 1969*b*) (and to a lesser extent that of *Ornitholestes** [Ostrom 1976*a*], *Compsognathus* [Ostrom 1978], Caenagnathidae [Barsbold 1983], and Avialae [Fig. 6P]) is a secondary modification (see Part V, character 84).

33) Fifth metatarsal reduced to no more than a spur of bone in adult. Pedal digit five is reduced and bears only a vestigial phalanx on the distal end of the fifth metatarsal in Dinosauria ancestrally (Fig. 6L, N). In contrast, no theropod has more than a vestigial metatarsal spur (Fig. 6O, P); the element has been lost in adult Ornithurae, and it may also have been lost in some ornithomimids, caenagnathids, and elmisaurids*, although loss and nonpreservation cannot be distinguished in the extinct theropods. The fifth pedal digit is reduced to a spur of bone in Proterochampsidae, the sister-group of Archosauria (Gauthier 1984). Within Archosauria the same apomorphy appeared independently in four different groups: Crocodylomorpha, pterodactyloid Pterosauria, Ornithischia, and Theropoda. The fifth digit could have been reduced in the ancestral dinosaur and subsequently reevolved in Sauropodomorpha, which retains what appears to be the ancestral condition. Alternatively, the fifth digit could have been reduced twice, once in Ornithischia and once in Theropoda. Two evolutionary events are required in either case; unless one is willing to assume that convergence is more likely than reversal in evolution (or vice versa), the level of synapomorphy of this character must be considered ambiguous. Fortunately, this character is but one among many supporting theropod monophyly, and regardless of how it is optimized, it has no effect on the conclusions of this analysis. In this instance I accept convergence over reversal as an explanation of the distribution of this character among dinosaurs; this conclusion predicts that we will one day find a fifth digit like that seen in sauropodomorphs in either an ornithischian or a theropod (or both).

34) Theropod first metatarsal. In Archosauria ancestrally, metatarsal I articulates with the tarsus and it is proportioned much like the other metatarsals (Fig. 6J). This condition is retained in *Lagosuchus** (Fig. 6K), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Fig. 6L), Ornithischia ancestrally (Fig. 6M), and Sauropodomorpha (Fig. 6N). In contrast, the proximal portion of metatarsal I fails to contact the tarsus and the compressed and triangular shaft of the element is bound by connective tissue to the medial side of metatarsal II in *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), and Ceratosauria (Fig. 6O). Metatarsal I is even more broadly separated from the tarsus in Carnosauria (Osborn 1906; Lambe 1917; Gilmore 1920), *Compsognathus* (Fig. 6Q), Elmisauridae* (Sternberg 1932), Caenagnathidae (Barsbold 1983), Ornithomimidae (Barsbold 1983), Deinonychosauria (Ostrom 1969*b*), and Avialae (Fig. 6P). Tarsitano and Hecht (1980) argued that in Theropoda with an intact pes, metatarsal I is attached about half-

way down metatarsal II (Fig. 6O), and birds are further derived in that the element attaches about three-quarters of the way down metatarsal II (Fig. 6P). Ostrom (1976*a*) argued that a reversed hallux was ancestral for Theropoda. Tarsitano and Hecht (1980) took exception, noting that in the few articulated theropod feet, the hallux is short, unreversed, and metatarsal I lies medial to metatarsal II. I agree with Tarsitano and Hecht that the condition of the first digit as they describe it is indeed ancestral for Theropoda. However, the articulated feet of *Compsognathus* show that metatarsal I in this taxon is like that of birds, and unlike that of early theropods, in that it is short and displaced to the posterior side of metatarsal II (Fig. 6Q). The reversal, elongation, and posterior displacement of the hallux presumably relate to the perfection of the grasping function of the foot in Avialae (see Part V, character 84). Tarsitano and Hecht (1980) argued that this functional complex is not ancestral for Theropoda and I quite agree. Nevertheless, it is clear that certain modifications that are prerequisite to the reversed hallux of Avialae apply to more inclusive groups of Theropoda than to birds alone. In this regard, it is interesting to note that the first pedal digit recapitulates its phylogenetic history in the development of the pes in extant Aves (Heilmann 1926). The position of the first pedal digit as preserved in early theropods indicates that this digit was unreversed, at least at rest. However, as Thulborn (1984) has noted, Triassic theropod trackways displaying impressions of reversed first digits stand as mute testaments to our inability to infer function from structure alone.

35) Thin-walled long bones (=hollow skeleton). This character has long been recognized as a theropod synapomorphy (see diagnosis of "Theropoda" in Marsh 1881*b*, 1884*a*) and it is present in all taxa here considered to be theropods except for Hesperornithes and a few other diving birds. The walls of the long bones are thicker in *Dilophosaurus* and *Ceratosaurus*, and even thicker in Carnosauria, as their larger size demands. Even so, the limb bones of the largest theropod, *Tyrannosaurus rex*, are thin-walled in comparison to the same elements of contemporaneous large dinosaurs, such as *Triceratops* and *Anatosaurus* (pers. obs.). The limb bones are hollow in Dinosauria ancestrally, but aside from Pterosauria (Bramwell and Whitfield 1974), no other archosaurs have long bones that are quite as thin-walled as those of Theropoda (Romer 1956). Moreover, T. Rowe (pers. comm.) has pointed out that in theropods the entire skeleton, including the phalanges and caudal vertebrae, are hollow and lightly constructed in comparison to other dinosaurs of equal size. This may partly explain why theropods in general and birds in particular are so uncommon in the fossil record.

III. Phylogenetic Relationships within Tetanurae

Tetanurae (n. txn.)

(Gr.: *tetanos*, stiff; *ourae*, tails)

Temporal Range.—late Jurassic to Recent.

Included Taxa.—Carnosauria, *Compsognathus*, *Ornitholestes**, *Coelurus**, *Microvenator**, *Saurornitholestes**, *Hulsanpes*, Elmisauridae*, Caenagnathidae, Ornithomimidae, Deinonychosauria, and Avialae.

Diagnosis.—Tetanurae is defined here to include birds and all other theropods that are closer to birds than they are to Ceratosauria. In the following analysis, Ceratosauria, Sauropodomorpha, Ornithischia, Herrerasauridae*, Pterosauria-*Lagosuchus**, Ornithosuchidae, *Euparkeria**, and Pseudosuchia will be used as successively more remote outgroups. Tetanurine theropods are diagnosed by the following synapomorphies.

36) Absence of enlarged fanglike tooth in dentary. Gauthier (1984) proposed that an unnamed taxon including erythrosuchids, proterochampsids, and archosaurs (n. comb.) can be distinguished among Archosauromorpha by an enlarged anterior dentary tooth (e.g., Fig. 1A, B). The fanglike tooth projects dorsally between teeth in the upper tooth-bearing bones, and it may be received in a more or less pronounced notch between the premaxilla and maxilla. The ancestral condition is retained by *Liliensternus** (Huene 1934) and, in a modified form, by Ceratosauria. The fang is very large in ceratosaur theropods, and it is received into the diagnostic subnarial gap in all ceratosaurs except *Ceratosaurus* (pers. obs.; Welles 1984). In contrast, an enlarged dentary fang is absent in Carnosauria (Fig. 1G, H), *Compsognathus* (Ostrom 1978), Elmisauridae* (Gilmore 1924), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 1J, K), and Avialae (Fig. 1L). This character is considered indeterminable in the toothless Ornithomimidae (Fig. 1I) and Caenagnathidae (Osmolska 1976).

37) Maxillary fenestra large and posteriorly placed. An antorbital fenestra was present in the ancestral archosaur, and this condition was retained by the ancestral dinosaur (Romer 1956). Theropods differ in that they possess an additional fenestra anterior to the antorbital fenestra, here termed the maxillary fenestra (=second antorbital fenestra of various authors; see Madsen 1976:65, plate 6). In contrast to the small, slitlike fenestra confined to the anterior margin of the antorbital fossa in Ceratosauria (Welles 1984), however, the maxillary fenestra is large, circular, and more posteriorly placed in Carnosauria (Fig. 1G, H), Ornithomimidae (Fig. 1I), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), Deinonychosauria (Fig. 1J, K), and *Archaeopteryx** (Fig. 1L). The maxillary fenestra is absent in the highly modified antorbital region of Ornithurae. A second pre-antorbital fenestra is present in some Rauisuchia (Sill 1974) and in a single erythrosuchid, *Shansisuchus* (Young 1964). However, this fenestra lies between the premaxilla and maxilla, and it is not considered homologous with the maxillary fenestra present in Tetanurae.

38) Antorbital tooth row. In Saurischia ancestrally the upper and lower tooth rows terminate below the center of the orbit (Fig. 1A–F). The ancestral condition is retained in *Procompsognathus** (pers. obs.) and Ceratosauria (Colbert and Russell 1969). In contrast, the tooth rows are entirely antorbital in Carnosauria (Fig. 1G, H), Deinonychosauria (Fig. 1J, K), *Ornitholestes** (Osborn 1903, 1917), *Compsognathus** (Ostrom 1978), and Avialae ancestrally (Fig. 1L). In the context of all the evidence, the most parsimonious explanation for the edentulous Ornithomimidae, Caenagnathidae, and Aves is that they each achieved their toothless condition separately, and that they did so via the condition seen in other tetanurine theropods. Antorbital tooth rows arose independently in several groups of diapsids, most of which are carnivores (e.g., McDowell and Bogert 1954). However, some herbivores, for example some sauropods and ceratopsian ornithischians, have also acquired this condition. An antorbital tooth row also occurs in a variety of other archosaurs that are thought to have been carnivorous, such as some erythrosuchids (Charig and Reig 1970), rauisuchians (Bonaparte 1981), and some pterosaurs (Wellnhofer 1978), but it

is absent in others, such as ornithosuchids (Walker 1964) and proterosuchids (Cruickshank 1972). Thus, while the character is not an infallible indicator, it appears to be correlated with macropredaceous habits (sensu McDowell and Bogert 1954).

39) Spine table on the axis. Spine tables are present in the posterior cervicals and anterior trunk vertebrae in Archosauria ancestrally (Gauthier 1984). However, spine tables are absent in the anterior cervicals including the axis in Pseudosuchia (Romer 1956), *Euparkeria** (Ewer 1965), Ornithosuchidae (Bonaparte 1975*b*), *Lagosuchus** (Bonaparte 1975*b*), Pterosauria (Wellnhofer 1978), Herrerasauridae* (Galton 1977), Ornithischia (Santa Luca 1980), Sauropodomorpha (Fig. 3D), *Liliensternus** (Huene 1934), and Ceratosauria (Fig. 3E). Thus, anterior spine tables are absent in theropods ancestrally. In contrast, an expanded distal end of the neural spine (=spine table) is present, at least on the axis, in Carnosauria (Madsen 1976), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 3F, H), and Avialae (Fig. 3G, I).

40) Transition point begins closer to proximal half of tail. With the exception of a few birds lacking the pygostyle, all theropods have tails that are mobile proximally and stiffened distally. The transition between these regions is marked by roughly coincident changes in neural spines, transverse processes, haemal arches, and pre- and postzygapophyses, which are referred to collectively as the transition point. As noted above, although ceratosaurs display the transition point, it is less marked, and they retain the ancestral condition of the caudal haemal arches well into the posterior half of the tail. In contrast to ceratosaurs, however, the transition between the stouter and more mobile proximal and stiffened and thinned distal portions of the tail is more pronounced and begins closer to the base of the tail in tetanurine theropods. In addition, unlike the case in Ceratosauria (Gilmore 1920), the haemal arches in Carnosauria (Madsen 1976), Ornithomimidae (Fig. 2E), Deinonychosauria (Fig. 2G), and Avialae ancestrally (Fig. 2F) become progressively shorter dorsoventrally and elongate anteroposteriorly from the proximal to the distal end of the tail. Russell (1972) noted some variation in the position of the transition point in the tails of taxa that I include in Tetanurae, and detailed comparisons of theropod caudal series may provide further characters for phylogenetic analysis. Analogous modifications of the caudal region are present in sand lizards, such as *Callisaurus, Cophosaurus,* and *Holbrookia* (pers. obs.). The zygapophyses are not deeply imbricate as in theropods, but they are vertically disposed (as in most ornithodiran archosaurs); the tail is stout basally, but it tapers abruptly in a region analogous to the theropod transition point, and the greater part of the tail is thin, with short haemal arches that are expanded fore and aft. Thus, the base of the sand lizard tail would correspond to the mobile proximal portion, and the remainder of the tail to the stiff distal portion, of the tetanurine tail. Sand lizards typically curl their comparatively short tails dorsally, particularly during bipedal progression when the tail acts as a dynamic stabilizer. The tail is also used for display, with side-to-side wagging of the curled distal portion playing a role in social interaction. The stiffened distal portion of the theropod tail probably could not have been curled as in sand lizards, owing to the deeply imbricate zygapophyses. Although the theropod tail's paramount role may have been as a dynamic stabilizer, one cannot overlook the possibility of accessory roles in social display.

41) Scapula straplike. As in Diapsida generally, the distal end of the scapula is flared anteroposteriorly in Dinosauria ancestrally (Fig. 4A, B). This condition is retained by Ceratosauria (Raath 1969; Welles 1984) and from what remains of the scapula in *Liliensternus** (Huene 1934), it appears to retain the ancestral condition as well. In contrast, the distal expansion is reduced or absent and the scapula is thus straplike in Carnosauria (Madsen 1976), *Compsognathus* (Ostrom 1978), *Ornitholestes** (Ostrom 1976*a*), Ornithomimidae (Fig. 4C), Deinonychosauria (Ostrom 1976*a*), and Avialae (Fig. 4D). This modification is further enhanced in Ornithurae, in which the scapula tapers distally (Elzanowski 1981). The carnosaur *Tyrannosaurus* is unusual among tetanurines in the possession of a flared distal end of the scapula (Osborn 1906); rather than symmetrical, however, the scapula is flared mainly at its anterior margin, suggesting that this condition is secondary.

42) Coracoid tapers posteriorly in profile. In Ornithodira ancestrally the profile of the coracoid is subcircular below its articulation with the scapula, although the element may taper to a blunted point posteroventrally. The ancestral condition is retained in Ornithischia (Fig. 4A), Sauropodomorpha (Fig. 4B), and in Theropoda ancestrally in that the coracoid has a subcircular profile in *Liliensternus** (Huene 1934) and Ceratosauria (Welles 1984). In contrast, the pointed posteroventral margin of the coracoid is more pronounced in that it extends well beyond the rims of the glenoid when the scapulocoracoid is oriented vertically in Carnosauria (Madsen 1976), *Compsognathus* (Bidar et al. 1972), and Ornithomimidae (Fig. 4C). The rectangular profile of deinonychosaurs and avialans is here considered a further modification of the form of the coracoid seen in other tetanurine theropods. A posteriorly tapering coracoid appeared independently in ornithopod ornithischians (e.g., Galton 1974).

43) Manus forms more than two-thirds of combined lengths of radius plus humerus. Ostrom (1969*b*) pointed out that the manus is less than half the length of the humerus plus radius in Ceratosauria (47% in *Coelophysis* and *Syntarsus*), as it is in Dinosauria ancestrally. *Heterodontosaurus tucki* is exceptional among ornithischians in that the manus is over half (i.e., 56%) of the humerus plus radius length (Santa Luca 1980). In contrast, Tetanurae possesses conspicuously enlarged hands. The manus is 77% of the length of the radius plus humerus in Carnosauria ancestrally (i.e., *Allosaurus*), although the forearm is greatly reduced in Tyrannosauridae (Lambe 1917). The manus is modified in Ornithomimidae, but it is still at least 58% of the length of the radius plus humerus. In Caenagnathidae (Osborn 1924*b*), *Ornitholestes** (Osborn 1917), Deinonychosauria (Ostrom 1969*b*), and Avialae (Ostrom 1976*a*) ancestrally, the manus is 67–75% of the humerus plus radius length. Tetanurae in general and coelurosaurs in particular are unique among Dinosauria in the relative size of the hand. Although *Scleromochlus** does not appear to be so modified (Huene 1914*a*), pterosaurs are the only other archosaurs whose hands exceed the relative size seen in Tetanurae. Even the highly modified hands of Ornithurae are enormous relative to those of most other archosaurs.

44) Basal half of metacarpal I closely appressed to metacarpal II. As in Diapsida ancestrally, the metacarpals overlap one another proximally, and this condition is retained in Pseudosuchia (Fig. 4G), Ornithosuchidae (Walker 1964), Pterosauria (Wellnhofer 1978), Ornithischia (Fig. 4H), Sauropodomorpha

(Fig. 4I, J), and Ceratosauria (Welles 1984). In contrast, the bases of metacarpals I and II are closely appressed for at least half the length of metacarpal I in Carnosauria (Fig. 4L), Ornithomimidae (Fig. 4M), *Ornitholestes** (Osborn 1917), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O).

45) Base of metacarpal III set on palmar surface of hand below base of metacarpal II. As was argued in Part I, character nine above, the bases of metacarpals IV and V (and thus their associated digits), were set on the palmar surface of the hand in Saurischia ancestrally. Tetanurine theropods are further specialized within this assemblage in that metacarpal III is also displaced ventrally with respect to metacarpal II. Ceratosauria retains the ancestral condition (Fig. 4K), but the derived condition is present in Carnosauria (Fig. 4L), Ornithomimidae (Fig. 4M), Elimsauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). Even in disarticulated specimens, the beveled articular surface of the proximal end of metacarpal III is sufficient to identify this character.

46) Fourth manal digit absent beyond embryonic stages. As argued above, the fourth manal digit is reduced in all Theropoda and probably plays no role in the function of the hand (Galton 1971). Unlike Ceratosauria, however, the fourth digit is absent in Carnosauria (Fig. 4L), *Compsognathus* (Ostrom 1978), *Saurornitholestes** (Sues 1978), Elmisauridae* (Osmolska 1981), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 4M), and Deinonychosauria (Fig. 4N). Osborn (1917) and Ostrom (1969*b*) identified a fragment of bone near the proximal end of metacarpal III in *Ornitholestes** that may represent a vestige of metacarpal IV. The fourth digit is absent in all adult Avialae (Fig. 4O) but the precursor of the element is reported in embryonic Aves (Heilmann 1926; see Hinchliffe and Hecht 1984, for an alternative view).

47) Obturator process on ischium. An obturator process on the ischium is absent in Pseudosuchia, Ornithosuchidae, *Lagosuchus**, Pterosauria, and Herrerasauridae* (Gauthier 1984). An obturator process is also absent in all Ornithischia (Fig. 5A) except for *Lesothosaurus* (Thulborn 1972) and Ornithopoda (sensu Santa Luca 1980), and it is absent in Sauropodomorpha (Fig. 5B), *Liliensternus** (Huene 1934), *Procompsognathus** (Ostrom 1981), and Ceratosauria (Fig. 5C). In contrast, an obturator process is present on the ischium of Carnosauria (Fig. 5D), Ornithomimidae (Fig. 5E), *Ornitholestes** (Osborn 1917), *Compsognathus* (Ostrom 1978), Elmisauridae* (P. J. Currie, pers. comm.), Caenagnathidae (Barsbold 1983), and Deinonychosauria (Fig. 5F, G). Ostrom (1976*a*:129) may be correct in interpreting the anterior of the two processes at the ventral extremity of the ischium of *Archaeopteryx** as an obturator process (Fig. 5H). The ischium of *Archaeopteryx** is, however, difficult to assess because the element is in several ways different from that seen in other Theropoda, including Ornithurae (Fig. 5I; Tarsitano and Hecht 1980). Unlike the pubis in *Archaeopteryx**, the morphology of the ischium has not received much attention, and this element needs further study. Nevertheless, even if the lower process on the ischium is not homologous with the obturator process of other Tetanurae, it is still more parsimonious to accept that birds lost, rather than never had, an obturator process.

48) Expanded pubic foot. An expanded distal extremity of the pubis is present in Herrerasauridae* (Reig 1963; Benedetto 1973; Cooper 1981*a;* Galton 1977). However, the apomorphy is unknown elsewhere among Dinosauria, including *Liliensternus** (Huene 1934) and Ceratosauria (Fig. 5C). Thus, an expanded pubic foot applies to Herrerasauridae* on one hand, and Tetanurae on the other, but not to a group including both. An expanded foot at the distal end of the pubis is present in Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), Ornithomimidae (Fig. 5E), *Microvenator** (Ostrom 1970), *Compsognathus** (Ostrom 1978), *Coelurus** (Marsh 1896), Deinonychosauria (Fig. 5F, G), and *Archaeopteryx** (Fig. 5H). Thus, the absence of a pubic foot in Ornithurae is considered secondary (Fig. 5I).

49) Femur with winglike anterior (=lesser) trochanter. The anterior trochanter is a spikelike ridge in Dinosauria ancestrally, and this condition is retained in *Liliensternus** (Huene 1934) and in a modified form in Ceratosauria (Raath 1969). In contrast, the anterior trochanter is prominent and winglike in Carnosauria (Madsen 1976), Elmisauridae* (P. J. Currie, pers. comm.), Ornithomimidae (Osmolska et al. 1972), *Microvenator** (Ostrom 1970), and in a modified form in Deinonychosauria and Avialae (Ostrom 1976*a,* 1976*b;* Padian 1982). It is interesting to note at this point that a discrete, winglike lesser trochanter occasionally appears as a variant in a few extant birds. A winglike anterior trochanter arose convergently in Ornithischia, and it is particularly prominent in Ornithopoda (sensu Santa Luca 1980; e.g., Galton 1974). Evidently, the dorsal migration and posterior displacement of the area of insertion of the so-called M. iliotrochantericus group of Aves (Cracraft 1971), is associated with perfection of bipedal, cursorial habits (Coombs 1978*b;* see further discussion in Part V, character 82).

50) Ascending process of astragalus tall, broad, and superficially placed. Welles and Long (1974) provided a detailed description of the theropod tarsus. The distribution of characters in their classification of theropod tarsi (p. 197) indicates that their five "distinct kinds" are phenetic, rather than phylogenetic, concepts. For example, they note that one of the characters, the "free medial component" (=superficial part of ascending process) is absent both in dinosaurs ancestrally and in their "ceratosauroid" group of theropods (=*Liliensternus** and Ceratosauria of this work). The "free medial component" is, however, present in all members of their "allosauroid" (Fig. 6A), "albertosauroid," "tyrannosauroid," and "ornithomimoid" (Fig. 6B, C) groups, as well as in *Compsognathus, Ornitholestes**, and *Microvenator**. Moreover, an ascending process is present in all birds (Fig. 6D), and although its height and width may vary with size and the presence of a tendinal groove in birds, it is relatively larger in birds than it is in theropods ancestrally (pers. obs.). Accordingly, the development of a larger ascending process is considered to be a synapomorphy of Tetanurae. Although the ascending process, which arises as a separate ossification center in Theropoda (Heilmann 1926; Welles 1983; pers. obs.), retains its ancestral relations with the tibia, it has shifted its association with the proximal tarsals in Neognathae (pers. obs.).

51) Metatarsals II and IV with broader participation in ankle and metatarsal III compressed between them to a variable degree. Using the ornithopod ornithischian *Hypsilophodon** (Fig. 6E), the sauropodomorph *Massospondylus* (Cooper 1981*a*), the early theropod *Liliensternus** (Huene 1934), and the ceratosaur *Dilophosaurus* (Fig. 6F) to assess the ancestral condition of the

metatarsus in Saurischia, neither metatarsal II or IV contributes as much to the surface area of the ankle joint as does metatarsal III in proximal view. In contrast, metatarsals II and IV participate more broadly in the ankle relative to metatarsal III, and metatarsal III is more or less compressed between II and IV. The width of metatarsal III is more than 33% of the width of metatarsals II–IV on the midline in Ornithischia (Fig. 6E) and Ceratosauria (Fig. 6F) and it is less than 26% of the width of the proximal ends of these metatarsals in Carnosauria (Fig. 6G), *Hulsanpes* (Osmolska 1982), Elmisauridae* (Osmolska 1981), Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Fig. 6H), and Avialae (Fig. 6I; see Part IV, character 67, for further discussion).

52) Metatarsal I short. As noted above, metatarsal I does not reach the tarsus in theropods ancestrally. In the ancestral condition, the compressed shaft of metatarsal I is relatively long, as can be seen in *Liliensternus** (Huene 1934), *Procompsognathus** (pers. obs.), and Ceratosauria (Fig. 6O) with the possible exception of *Ceratosaurus* (see Gilmore 1920). By contrast, metatarsal I in Tetanurae is relatively short (e.g., Fig. 6P). The apomorphic tetanurine condition is reported in Carnosauria (Lambe 1917), *Compsognathus* (Fig. 6Q), Caenagnathidae (Barsbold 1983), Elmisauridae* (Sternberg 1932), Ornithomimidae (Barsbold 1983), Deinonychosauria (Ostrom 1969*b*), and Avialae (Fig. 6P).

IV. Phylogenetic Relationships within Coelurosauria

Coelurosauria (n. comb.)

Temporal Range.—late Jurassic to Recent.

Included Taxa.—*Ornitholestes**, *Compsognathus*, *Microvenator**, *Coelurus**, *Saurornitholestes**, *Hulsanpes*, Elmisauridae*, Caenagnathidae, Ornithomimidae, Deinonychosauria, and Avialae.

Diagnosis.—As defined here, Coelurosauria includes birds and all other theropods that are closer to birds than they are to Carnosauria. This concept differs fundamentally from that of previous workers, all of whom applied "coelurosaurs" to a paraphyletic group including all theropods except for carnosaurs. In the following analysis, Carnosauria, Ceratosauria, Sauropodomorpha, Ornithischia, and Herrerasauridae* will be used as successively more remote outgroups. The remaining outgroups, Pterosauria-*Lagosuchus**, Ornithosuchidae, *Euparkeria**, and Pseudosuchia, will be referred to as the "nondinosaurian archosaurs" or "other archosaurs" to facilitate the following discussion. Coelurosauria possesses the following synapomorphies distinguishing it among Theropoda.

53) Subsidiary fenestra between pterygoid and palatine. A subsidiary fenestra is absent in nondinosaurian archosaurs (Romer 1956), Ornithischia (e.g., Heaton 1972), and Sauropodomorpha (Galton 1984). According to Colbert and Russell (1969), this character is also absent in taxa here referred to Ceratosauria and Carnosauria. In contrast, a subsidiary fenestra between the pterygoid and palatine is present in Ornithomimidae (Osmolska et al. 1972), Caenagnathidae (Osmolska 1976), and Deinonychosauria (Colbert and Russell 1969). The palate is not exposed in *Archaeopteryx**, and the palate of other birds is too transformed to interpret in this regard (McDowell 1978). In the context of all the evidence, birds are considered to have modified the palatal elements from the condition seen in other coelurosaurs.

54) Deeply excavated pocket on ventral surface of ectopterygoid flange. As noted above (Part II, character 15), a relatively smaller excavation is present on the ventral surface of the ectopterygoid in Carnosauria (Colbert and Russell 1969). According to Sues (1978) this pocket is deeper in *Saurornitholestes**, Ornithomimidae, and Dromaeosauridae, and the apomorphic condition appears to obtain as well in Troodontidae (Barsbold 1983) and Caenagnathidae (Osmolska 1976). As in the case of the previous character, modification of the avian palate precludes a simple conclusion regarding the presence or absence of this character, especially since the ectopterygoid has not been identified in birds. Nevertheless, in view of their relationships within Coelurosauria it would still be simpler to accept secondary modification in birds. Another modification in this region of the palate may also be diagnostic of Coelurosauria: a conspicuous oval depression, subdivided by a ridge, that lies on the dorsal surface of the pterygoid process of the ectopterygoid in the dromaeosaur *Deinonychus* and in *Saurornitholestes** (Sues 1978). Although at present this character has been reported only in these taxa, it is absent in Carnosauria, indicating that it arose within theropods after the divergence of carnosaurs; more information will be necessary to establish its level of synapomorphy.

55) Cervical ribs fused to centra in adults. Cervical ribs remain unfused throughout ontogeny in nondinosaurian archosaurs aside from some Pterosauria (Romer 1956). Both Ornithischia and Sauropodomorpha retain the ancestral condition, although fusion between ribs and vertebrae in the cervical region arose within Sauropoda. Fully adult ceratosaurs, such as the specimens of *Syntarsus* and *Ceratosaurus* described by Raath (1969) and Gilmore (1920) respectively, retain free ribs, and this appears to be the case in *Allosaurus* as well (Madsen 1976). Thus, the ancestral condition in tetanurine theropods appears to be the retention of free cervical ribs in adults. Fused cervical ribs have so far been reported only in *Coelurus** (Marsh 1881*a*), fully adult specimens of ornithomimids such as *Gallimimus* (Osmolska et al. 1972) and *Struthiomimus* (Osborn 1917), and in fully adult ornithurine birds (Marsh 1880). *Coelurus** is too poorly known to allow placement beyond Coelurosauria *incertae sedis*, and will for that reason be ignored in the following discussion.

At first glance, it seems that fused cervical ribs arose (at least) twice, once in Ornithomimidae and once in Ornithurae, because neither *Archaeopteryx** nor deinonychosaurs are reported to have fused cervical ribs. This interpretation itself depends on assuming that there are fully adult examples among the known specimens of the latter two taxa, and according to the criteria here used to determine cessation of growth, this does not appear to be the case. The situation is further complicated by the fact that *Deinonychus* is the only deinonychosaur for which any portion of the cervical region has been described, and these specimens represent subadult individuals. For example, the axial intercentrum remains suturally distinct from both the first and second centrum (Fig. 3F), while in fully adult reptiles (sensu Gauthier et al., in prep.) the second intercentrum is always fused, at least to the first centrum. Although this fusion takes place earlier in ontogeny in some reptiles (e.g., in extant crocodylomorph embryos), it may be a near terminal event in the skeletal ontogeny of others (e.g., most squamates), but by the cessation of growth it is in any case fused. Fusion of the axial intercentrum

takes place prior to fusion of the cervical ribs in extant birds (pers. obs.); thus the absence of fused cervical ribs in the currently known *Deinonychus* may simply reflect the relative immaturity of the specimens, not the retention of an ancestral condition. The presence or absence of this character will be scored as unknown in Deinonychosauria.

For similar reasons, I also consider this character indeterminate in *Archaeopteryx**. If the five *Archaeopteryx** skeletons are ranked according to measures of homologous structures, the relative size from largest to smallest specimens would be the subequal-sized London, Maxberg, and Haarlem specimens, followed by the Berlin, and then the Eichstätt specimens (see Wellnhofer 1974). The first three specimens are of comparable size, the Berlin specimen is about 15% smaller than the London specimen, and the Eichstätt is about 45% smaller than the London specimen, based on the length of the humerus (data from Wellnhofer 1974). The scapula and coracoid are unfused in all specimens, although they are firmly attached to one another in the London specimen, indicating by extrapolation that the London, Maxberg, and Haarlem specimens are near to full maturity (also corroborated by fusion of tarsometatarsus). Unfortunately, the cervicals are either poorly preserved or absent in these apparently full-grown specimens. Free cervical ribs are present in the smaller specimens from Berlin and Eichstätt, but this is to be expected in view of the apparent immaturity of these specimens. Thus, until this character can be determined in new and fully adult specimens of *Archaeopteryx** and Deinonychosauria, it is simpler to accept that fusion of cervical ribs, at least by maximum adult size, is synapomorphic of Coelurosauria among Theropoda.

56) Cervical zygapophyses flexed. In nondinosaurian archosaurs, the cervical zygapophyses are planar (pers. obs.), and this condition is retained in Ornithischia (e.g., Ostrom 1970), Sauropodomorpha (Huene 1908), Ceratosauria (Gilmore 1920), and Carnosauria (Madsen 1976). Thus, planar zygapophysial facets in the cervical region are the ancestral condition in Tetanurae. In contrast, the zygapophysial facets are sharply flexed about a line dividing the facet into larger lateral and smaller medial components in Ornithomimidae (Osmolska et al. 1972), Deinonychosauria (Ostrom 1969*b*), and Avialae (this character is not determinable in *Archaeopteryx**, but it is present in other birds).

57) Anterior cervical vertebrae broader than deep anteriorly, with kidney-shaped articular surfaces that are taller laterally than on the midline. Amphicoelous intervertebral joints are the ancestral condition for Archosauria (Romer 1956). Either the ancestral condition, or a more or less prominent opisthocoely derived from it, is retained in Ornithischia (Galton 1974), Sauropodomorpha (Huene 1932), *Liliensternus** (Huene 1934), Ceratosauria (Gilmore 1920), and Carnosauria (Madsen 1976). Unfortunately, the placement within the neck of isolated cervicals referred to *Coelurus** (Marsh 1881*a*) and *Microvenator** (Ostrom 1970) is unknown. In contrast to the ancestral condition, the anterior articular surfaces in the anterior cervical vertebrae of Ornithomimidae (Osmolska et al. 1972) and Deinonychosauria (Fig. 3H) are modified in a distinctly avian manner, although the posterior surfaces remain amphicoelous (Ostrom 1969*b;* posterior amphicoely led de Beer 1954, to the erroneous conclusion that the London *Archaeopteryx** was amphicoelous throughout the column). The kidney-shaped anterior surfaces display the initial stages of avian heterocoely. They are not much less modified in this respect than are homologous vertebrae of *Ichthyornis* (Marsh 1880), early Hesperornithes such as *Baptornis* (Martin and Tate 1976), and embryos of extant birds (pers. obs.). L. D. Martin (pers. comm.) notes that heterocoely becomes more pronounced and extends further posteriorly in the vertebral column within Hesperornithes, and that these same modifications arose in parallel in Aves ancestrally. Thus, the fully heterocoelous condition so characteristic of extant birds (e.g., Fig. 3I), arose twice within Ornithurae.

58) Furcula. In Dinosauria ancestrally the clavicles are reduced and gracile, and they are difficult to distinguish from ribs in all but perfectly articulated fossils (Ostrom 1976*a*). Clavicles are present in the ceratosaur *Segisaurus** (Camp 1936; pers. obs.), but they have yet to be identified in Carnosauria, in which the forelimbs and girdles are reduced (Lambe 1917). Fused clavicles (=furcula) have been reported in Caenagnathidae and Ornithomimidae (Barsbold 1983), and these furcula are like those of *Archaeopteryx** in that they are very robust, unlike clavicles in dinosaurs ancestrally, or for that matter in Ornithurae of equivalent size (see following character for comments on functional implications of a robust furcula). Fusion of the clavicles takes place during postnatal ontogeny in extant birds (pers. obs.). The timing of this event is unknown in coelurosaurs ancestrally, but fusion of the clavicles would probably have occurred no earlier in the ontogeny of extinct than extant coelurosaurs. Clavicles have yet to be described in Deinonychosauria, although they are said to be present in *Velociraptor* (Kielan-Jaworowska and Barsbold 1972). Fused clavicles are also present in Avialae ancestrally (Heilmann 1926), although the elements may be reduced and unfused, or absent, via paedomorphosis, in flightless taxa within this group (Marsh 1880; Glenny and Friedmann 1954; Van Tyne and Berger 1959). Based on the development of *Coturnix*, Lansdown (1968) suggested that the avian furcula may be a neomorph because at least part of the element forms from a cartilaginous precursor. Clavicle development in *Coturnix* was, however, recently reconsidered by Russell and Joffe (1985), and they reaffirmed that the element was dermal rather than endochondral in origin.

59) Bony sternal plates fused, at least in fully adult individuals. Another character that may be functionally related to the development of the furcula, namely, a fused, bony sternum, may have originated at a level more inclusive than Ornithurae within Coelurosauria. Olson and Feduccia (1979) argued that the robust furcula of *Archaeopteryx**, together with the coracoclavicular membrane, acted as the point of origin of the muscle providing the power stroke for the wing, a hypertrophied M. pectoralis. They further noted that the posterior portion of this muscle also originates from the area of the sternum that is not preempted by the underlying M. supracoracoideus in Ornithurae. They presumed this portion of the M. pectoralis to be absent in *Archaeopteryx**, because *Archaeopteryx** was thought to lack a bony sternum. More recent finds allow us to modify Olson and Feduccia's conclusions.

Although the sternum may calcify in fully adult specimens, ossified sternal plates are absent in all nondinosaurian archosaurs (except Pterosauria). Paired ossifications within the cartilaginous sternum homologous with the pleurosteons of extant Aves have been reported in some subgroups of Ornithischia and Sauropodomorpha; but it is not clear if such ossifications were

present in these groups ancestrally (Romer 1956). Ossified sterna are unknown in early theropods, but more complete knowledge of this region in well-preserved ceratosaurs, such as *Coelophysis*, is necessary before absence can be distinguished from nonpreservation. The sternum becomes well ossified fairly late in posthatching ontogeny, it is superficially placed, and it is not attached to the remainder of the skeleton; this combination of factors makes the sternum a poor candidate for preservation. To date, paired sternal plates have only been reported in a single specimen of Carnosauria (Lambe 1917) and in a few specimens of Caenagnathidae, Ornithomimidae, and Deinonychosauria (Barsbold 1983). With the possible exception of the London specimen (de Beer 1954), bony sternal plates are unknown in *Archaeopteryx**. However, they remain as pleurosteons in juvenile Ornithurae, and may be accompanied by additional ossification centers, the lophosteon and metosteon, in the keel and xiphoid processes respectively (Bellairs and Jenkin 1960). Current knowledge of the distribution of this character among ornithosuchian archosaurs precludes a firm decision regarding the level of synapomorphy of this character. The boldest hypothesis would be that bony sternal plates arose in ancestral Ornithodira. An ossified sternum has long been considered synapomorphic for Ornithurae, especially since a bony sternum was thought to be absent in *Archaeopteryx**. However, in view of the presence of a bony sternum in other tetanurines, if not all ornithodirans, the sternum was probably present in *Archaeopteryx**; whether its absence results from nonpreservation or immaturity of the specimens, or a combination of both factors, cannot yet be determined. Whether or not fusion between the sternal plates is synapomorphic of Ornithurae is also questionable, because some caenagnathids (*Oviraptor*) and ornithomimids (*Ingenia*) also have fused sternal plates, at least in fully mature specimens (Barsbold 1983). Thus, this character appears to have arisen within Coelurosauria at a more inclusive level than birds alone. A sternum has so far been reported in only one deinonychosaur (*Velociraptor;* Barsbold 1983). The paired and apparently ancestral condition of the sternum in this taxon may not be conclusive, however, because the specimen has not been described completely enough to determine its stage of development. Full ossification of the sternal plates in extant birds occurs late in ontogeny, followed by coossification near maximum adult size (Bellairs and Jenkin 1960). Thus, the unfused sterna of *Velociraptor* may simply reflect immaturity. In view of the scant evidence, it may be too early to consider fusion of the sternum synapomorphic for Coelurosauria. In the context of the present hypothesis, however, I predict that a fused sternum will be found to have arisen outside of Ornithurae within Coelurosauria.

Such a find would have interesting consequences in light of arguments made by Olson and Feduccia (1979) regarding flight capability in *Archaeopteryx**. If, as seems to be the case, the basic pattern of the pectoral apparatus of *Archaeopteryx** applies to all Coelurosauria rather than to the immediate ancestor of Avialae, then some aspects of pectoral function must be equally general. That is to say, it would be inaccurate to consider the modifications of the pectoral girdle of *Archaeopteryx** solely in terms of flight. Thus, the presence of a hypertrophied M. pectoralis, as indicated by a robust furcula, enlarged coracoid, and fused sternum, suggests the presence of powerful forelimb adductors in all coelurosaurs. These modifications may have served initially to enhance the raptorial capabilities of coelurosaur forelimbs and only later been conscripted to serve the power stroke in avian flight. Aside from Coelurosauria, the only other archosaurs possessing a coossified, bony sternum are pterosaurs (Wellnhofer 1975, 1978), and this is hypothesized to be a case of convergence.

60) Elongate forelimb exceeds half the length of hindlimb and/or presacral vertebral column. Ostrom (1969*b*) pointed out that the forelimb is no more than 45% of the hindlimb length in Theropoda ancestrally. In Carnosauria, the forelimb varies from 25–42% of the hindlimb length. In contrast, Ornithomimidae (Russell 1972), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Ostrom 1969*b*), Deinonychosauria (Ostrom 1969*b*), and Avialae (Ostrom 1976*a*) are unique among Theropoda in that the forelimb exceeds 51% of the hindlimb length (Ostrom 1969*b*) and 52% of the presacral vertebral column (Cooper 1981*a*). The forelimbs of *Ornitholestes** and Deinonychosauria are at least 66% of hindlimb length and 75% of the presacral column, and the extremely long arms seen in many flying birds exceed the lengths of both the hindlimbs and the presacral vertebral column (Ostrom 1976*a*). Ostrom (1978) estimated the forelimbs of *Compsognathus* to be only 38% of hindlimb length. Yet in the context of all the evidence, the short forelimbs of *Compsognathus* are most parsimoniously interpreted as a secondary modification within coelurosaurs.

61) Manus gracile and elongate, especially digits two and three and their metacarpals, and metacarpal I only one-third the length of metacarpal II. As argued above, in Saurischia ancestrally metacarpal I is about half the length of metacarpal II. Moreover, the length of its second digit and its metacarpal is always less than seven times the width across the bases of metacarpals I and II. These relationships are retained in Ceratosauria (Fig. 4K) and Carnosauria ancestrally (Fig. 4L). In contrast, the hands are enormously elongate, and the length of the second digit and its metacarpal is at least nine times the width of metacarpals I and II in *Ornitholestes** (estimated from Ostrom 1976*a*), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), Deinonychosauria (Fig. 4N), and Avialae ancestrally (Fig. 4O). The characteristically modified manus of Ornithomimidae makes interpretation of the manus difficult. The length of the second digit and its metacarpal is over seven times the basal width of metacarpals I and II. However, metacarpal I is elongate and subequal in length to metacarpals II and III (Fig. 4M). This condition is unique among Theropoda in general and coelurosaurs in particular, because metacarpal I is only one-third of the length of metacarpal II in all other coelurosaurs, and it is no more than one-half of the length of metacarpal II in Saurischia ancestrally. In the context of all the evidence, the diagnostic modifications of the ornithomimid hand are hypothesized to be secondary.

62) Combined lengths of first and second phalanges of manal digit three less than or equal to length of third phalanx. As argued above, in Tetanurae ancestrally the first and second phalanges are relatively short compared to the length of the third (e.g., Fig. 4K, L). In contrast, the third phalanx equals or exceeds the combined lengths of the first and second phalanges in Ornithomimidae (Fig. 4M), Caenagnathidae (Barsbold 1983), Elmisauridae* (Osmolska 1981), *Ornitholestes** (Ostrom 1969*b*), Deinonychosauria (Fig. 4N), and Avialae ancestrally (Fig. 4O). The loss of all but the first phalanx of digit three in Ornithurae is considered secondary, but it is interesting to note that the

remaining phalanx is very short relative to the length of its metacarpal, just as in other coelurosaurs. This apomorphy arose convergently within Pterosauria (Wellnhofer 1978).

63) Fourth trochanter feebly developed or absent. A prominent fourth trochanter is the ancestral condition for Archosauria (Romer 1956). Moreover, an aliform fourth trochanter is the ancestral condition for Ornithodira (see Appendix A), and this condition is retained in *Procompsognathus** (Ostrom 1981), Ceratosauria (Welles 1984), and Carnosauria (Madsen 1976). In contrast, the fourth trochanter is represented by a feeble ridge in Ornithomimidae (Osmolska et al. 1972), or it may be absent, as in *Microvenator** (Ostrom 1970), Deinonychosauria (Ostrom 1976*b*), and Avialae ancestrally (Heilmann 1926; Tarsitano and Hecht 1980). This apomorphy arose convergently in Pterosauria (Wellnhofer 1978).

64) Moundlike greater trochanter (=posterior trochanter of Ostrom 1976*b*). The greater trochanter is represented by a rugose area on the posterolateral margin of the proximal end of the femur (in vertical pose) in Archosauria ancestrally (Romer 1923). The ancestral condition is retained by Ornithischia (Santa Luca 1980), Sauropodomorpha (Cooper 1981*a*), Ceratosauria (T. Rowe, pers. comm.), and Carnosauria (Madsen 1976). In contrast, a moundlike eminence develops within the greater trochanter in Ornithomimidae (pers. obs.), and Ostrom (1976*a*) has noted its presence in *Microvenator**, Deinonychosauria, and *Archaeopteryx**. Although lacking in many small birds, the greater trochanter appears to be modified with a moundlike eminence in at least some large ratites, such as *Dromaeus* (pers. obs.); thus the development of this feature may in part be size-related in extant birds.

65) Ascending process of astragalus enlarged both in height and width to cover most of anterodistal quarter of tibia. Welles and Long (1974) pointed out the synapomorphic resemblance among their "ornithomimoid" group (e.g., Fig. 6B, C), which with the addition of Avialae is equivalent to Coelurosauria as here defined. Birds present a problem in this regard, because several authors have claimed that the avian ascending process is not homologous with that seen in other Dinosauria (Whetstone and Martin 1979; Tarsitano and Hecht 1980; Martin et al. 1980; Martin 1983*a, b*). Tarsitano and Hecht (1980) even claimed that *Archaeopteryx** did not have an ascending process. My observations support the generally held view that an ascending process is present in *Archaeopteryx**. Moreover, Martin et al. (1980) used ultraviolet light to determine that the structure in question was not calcite as had been suggested by Tarsitano and Hecht (1980).

The development of the ascending process in Neognathae was most recently reviewed by Martin et al. (1980), who argued that the ascending process of birds is not homologous with that of other dinosaurs, because the ascending process arose in birds from a separate ossification center that fused to the calcaneum, rather than to the astragalus as in dinosaurs. This proposition requires reevaluation in light of further study. First, comparable developmental evidence from fossil theropods is lacking. Welles (1983) has, however, described a suture between the ascending process and astragalus in *Dilophosaurus*. Having examined the *Dilophosaurus* tarsi, it is difficult to distinguish the suture from cracks in the specimens. However, the orientation of the bone fibers on one margin of the so called "suture" are distinctly different from those in the underlying bone. Moreover, the ascending process appears to overlap the astragalus on the medial side of the proximal astragalar surface. In addition, Welles's interpretation of *Dilophosaurus* has been supported by examples of other nonavialan theropod tarsi (pers. obs.). More observations of other theropod fossils are necessary before we can confidently distinguish between cracks and sutures. Further examination of the ascending processes of other dinosaurs should be undertaken. Second, Martin et al. (1980) based their conclusion on the development of the tarsus in Neognathae, but the work of McGowan (1984) and my work with K. Warheit and K. de Queiroz shows that the condition in Neognathae is not ancestral for Aves. Indeed, all birds are like other dinosaurs in the possession of an ascending process; Ratitae and Tinami retain the ancestral condition in which the ascending process fuses to the astragalus, but Neognathae is specialized in that at least part of it fuses instead with the precocially developed calcaneum. Both Martin et al. (1980) and McGowan (1984) used the position of the ascending process with respect to the proximal tarsals as the only test for homology, and neglected the fact that this process has maintained its phylogenetic and ontogenetic association with the anterolateral margin of the distal end of the tibia throughout Dinosauria. Based on the study of avian tarsal ontogeny (Gauthier, Estes, and de Queiroz, in prep.), it is clear that the ancestral avian ascending process differs from that of other Coelurosauria only in that it is not so broad, although it may be as tall (e.g., *Struthio*).

The differences between the ascending processes of avialans (e.g., Fig. 6D) and other coelurosaurs appear to depend on two factors. One is that the size of the ascending process may vary with the size of the organism in question; the ossification center appears in the usual dinosaurian position, and during ontogeny this center grows both dorsally and medially, so that given enough time it would eventually cover the entire distal end of the tibia. This would account in part for the variation in size of the ascending processes of large and small birds.

The other factor affects the width but not the height of the ascending process in Ornithurae; that factor is the development of a prominent tendinal groove on the distal end of the tibia, which would limit the medial spread of the ascending process during ontogeny. The only other theropods with ascending processes with proportions like those of coelurosaurs are tyrannosaurid carnosaurs, and they are here considered to have acquired this condition separately.

It must be emphasized that even if Martin et al. (1980) were correct in assuming that the neognath condition was general among Aves, this assumption would not preclude close relationship between birds and other coelurosaurs. To argue that this region is "different" in birds, rather than ancestral to the condition of these elements in Theropoda, does not remove the possibility that birds possess a transformation of the condition seen in coelurosaurs generally. Birds are unlike other Diapsida in many details of the shape of the tibiotarsus and their ankles are in no sense ancestral to the condition seen in other Theropoda. In view of the numerous synapomorphies supporting the dinosaurian and coelurosaurian relationships of Aves, and the dearth of discordant data, it is more parsimonious to conclude that the smaller ascending process and its association with the enlarged calcaneum in Neognathae are secondary modifications.

66) Metatarsal I lies more on the posterior than the medial side of metatarsal II. As described above, coelurosaurs are fur-

ther derived within theropods (metatarsal I lies on the medial side of metatarsal II ancestrally) in that metatarsal I lies in a posteromedial position (e.g., Fig. 6Q). Wellnhofer (1974), Ostrom (1976*a*), and Tarsitano and Hecht (1980) noted the posterior position of metatarsal I in Avialae, although there was some disagreement among them as to the level at which this transformation took place within Theropoda. Once again, the controversy stems from different interpretations of the original positions of dissociated elements in fossils. This transformation is here considered to have taken place in the ancestral coelurosaur, because the apomorphic condition is known to be present in articulated examples of *Compsognathus* and Avialae. Moreover, articulated ceratosaurs demonstrate that this condition is not ancestral for Theropoda (pers. obs. of *Segisaurus**). The position of this element, however, remains a matter of conjecture in carnosaurs, and future finds may show that the apomorphic condition applies to a more inclusive taxon than to coelurosaurs alone among theropods. S. Hope (pers. comm.) notes that corvids have reversed the ancestral coelurosaur condition, because metatarsal I lies on the medial side of metatarsal II, as it does in Theropoda ancestrally.

67) Proximal surface of metatarsal IV subequal to II in size and metatarsal III more or less pinched between them. As argued above, the enlargement of the fourth metatarsal and the constriction of the proximal end of the third is the ancestral condition for Tetanurae. In contrast to Carnosauria ancestrally (Fig. 6G), however, metatarsal IV is subequal to III in size and metatarsal II forms no more than 22% of the width of the transverse axis of the ankle joint in Ornithomimidae (Osmolska et al. 1972). *Hulsanpes* (Osmolska 1982), *Compsognathus* (pers. obs.), Elmisauridae* (Osmolska 1981), Deinonychosauria (Fig. 6H), and Avialae (Fig. 6I). A further derived condition, in which the third metatarsal is so pinched between the second and fourth metatarsals that it barely contributes to the ankle joint, has arisen independently in tyrannosaurid carnosaurs, ornithomimids, *Hulsanpes*, troodontids, and elmisaurids*. Ornithurine birds are unusual in that the proximal end of metatarsal II lies behind the plane of metatarsals II and IV, but ornithurines are otherwise coelurosaurlike in sharing these apomorphies in metatarsal morphology.

V. Phylogenetic Relationships within Maniraptora

Maniraptora (n. txn.)

(Gr.: *manus*, hand; *raptus*, to seize)

Temporal Range.—late Jurassic to Recent

Included Taxa.—This taxon is erected to emphasize that all the characters listed below were shared by a common ancestor of Avialae and Deinonychosauria (or at least dromaeosaurs) that was not also an ancestor shared with Ornithomimidae. However, some of these characters also appear to be present in some of the less well known coelurosaurs, such as *Coelurus**, *Ornitholestes**, *Microvenator**, *Saurornitholestes**, *Hulsanpes*, Caenagnathidae, Elmisauridae*, and *Compsognathus*. Unfortunately, these taxa are too incompletely preserved to determine the sequence in which the maniraptoran synapomorphies appeared (see Fig. 9). A more precise determination of the level of synapomorphy of these characters must await future finds (see Conclusions, part I for further comment).

Diagnosis.—This section will examine the phylogenetic relationships between Deinonychosauria and Avialae. As in previous sections, evidence derived from less well known coelurosaurs listed above will be included. In the following analysis, Ornithomimidae, Carnosauria, Ceratosauria, and Sauropodomorpha will be used as successively more remote outgroups. Maniraptora possesses the following synapomorphies distinguishing this taxon among Theropoda.

68) Prefrontal reduced or absent. As in amniotes generally, both the lacrimal and prefrontal are present in Sauropodomorpha (Galton 1984). In Theropoda ancestrally the lacrimal gains broad exposure on the skull roof, thus partly replacing the prefrontal. The ancestral condition of the theropod lacrimal is retained by Ceratosauria (Gilmore 1920) and Carnosauria (Madsen 1976). This condition is also retained in Coelurosauria ancestrally, as is indicated by the presence of both elements in the growth series of the ornithomimid *Gallimimus* (Osmolska et al. 1972), and in all other ornithomimids in which this region is well preserved (Russell 1972). In contrast to the ancestral condition in coelurosaurs the prefrontal, if not absent, is at least reduced, its role in the construction of the skull roof having been supplanted by the lacrimal. The prefrontal is absent from all stages of ontogeny in Aves (Bellairs and Jenkin 1960), and no separate element is reported from this region in *Ornitholestes** (Osborn 1917) or Caenagnathidae (Barsbold 1983).

Currie (in press *a*) may have identified a prefrontal, albeit reduced and no longer in contact with the nasal, in *Troodon*. He notes that no clear suture remains because of coossification with the frontal. Nevertheless, he concludes that the structure is a prefrontal because its rugose dorsal surface bears shallow channels for blood vessels and its so-called "sutural contact" with the frontal is marked by several foramina. Currie notes further that at least remnants of sutural scars indicate the presence of a small and narrow prefrontal in *Dromaeosaurus*, *Sauronitholestes**, and perhaps in *Compsognathus*. However, the criteria Currie used to identify a prefrontal in *Troodon* may also be observed along the anterolaterally in ratites with subtriangular frontals. Moreover, the lateral margins of the frontal are similarly demarcated in tinamous; the dorsolateral surface is rugose and an apparent suture is formed by a series of foramina. The demarcated area often falls off when preparing the specimen, leaving traces of what could be considered a sutural surface. There is, however, no evidence that this structure represents a prefrontal bone. In both ratites and tinamous, the demarcation of the frontal in this region appears to be associated with the external nasal gland.

Aves is distinguished among extant tetrapods by the synapomorphic displacement of the external nasal gland to a position above the orbit. In birds in which the frontal reaches broadly over the orbits, the external nasal gland appears to induce the changes in frontal form noted above, including a linear array of more or less complete foramina marking the gland's position below the frontal margins (pers. obs.). (In some marine birds the dorsal surface of the frontal may display a foramen-filled trough that marks the dorsal displacement onto the frontal of a hypertrophied, salt-excreting external nasal gland.) Resolution of the problem of the identity of this structure will require more evidence. Nevertheless, whether one considers the structure a reduced prefrontal, or modification of the frontal induced by an avianlike position of the external nasal gland in maniraptorans, these theropods must be considered more birdlike in this respect than are other theropods.

Wellnhofer (1974), like some earlier authors, thought a separate prefrontal bone may have been present in the Eichstätt *Archaeopteryx**. Having examined this specimen, I am not con-

vinced of this interpretation, because the skull in general and the prefrontal region in particular are crushed and incompletely preserved. I agree with other authors that the portion of an element in the antorbital region on the counterslab is the remains of the lower ramus of the lacrimal, and I see no evidence of a separate prefrontal. Parts of the lacrimal remain in the antorbital region of the main slab, and there is a division between a fragment of the antorbital ramus and another fragment lying on the skull roof. The dispute centers on the identity of the latter fragment, and the conclusion that the division between the fragments on the main slab represents a suture rather than a break in an originally intact element. Given the direction in which the skull was compressed during preservation, the position and orientation of the division corresponds to a natural fracture plane between the skull roof and antorbital moieties of the usual maniraptoran lacrimal. Moreover, the shape and relationships of the so-called prefrontal are unlike those of other theropods, particularly since the "prefrontal" would exclude the lacrimal from the skull roof, unlike the case in any other theropod, including all other birds. Although there is some question about this character, it appears safe to conclude that unlike other theropods, the prefrontal is either reduced or lost in maniraptorans.

69) Axial epipophyses prominent. Epipophyses are present on the anterior cervicals in Saurischia ancestrally. In general the prominence of the epipophyses varies both with their position in the column and with the size of the saurischian in question. Nevertheless, in contrast to the condition of the axial epipophyses in Saurischia ancestrally (Fig. 3D, E), these structures are most prominent in Deinonychosauria (Fig. 3F) and Avialae (Fig. 3G), regardless of size.

70) Hypapophyses on vertebrae from cervicothoracic region. In Archosauria ancestrally the cervical vertebrae bear a more or less prominent midventral keel. The keel is commonly most prominent in the anterior elements of the cervical series, but it has become reduced or lost several times within Archosauria (Romer 1956). The keel is produced ventrally to form hypapophyses in eusuchian crocodylomorph pseudosuchians, but hypapophyses are otherwise absent in nondinosaurian archosaurs (Romer 1956). Hypapophyses are also absent in Sauropodomorpha (e.g., Galton and Cluver 1976), Ceratosauria (e.g., Gilmore 1920), and Carnosauria (e.g., Madsen 1976). The ancestral condition is retained in Coelurosauria in that hypapophyses are absent in Ornithomimidae (Osmolska et al. 1972) and *Compsognathus* (Ostrom 1978). In contrast, midventral keels in the anterior trunk vertebrae (i.e., cervicothoracic region) are produced ventrally to form discrete hypapophyses associated with the attachment of the M. longus colli ventralis in Deinonychosauria (Ostrom 1969*b*). The condition is not determinable in any of the *Archaeopteryx** specimens, but more or less prominent hypapophyses are present throughout Ornithurae (Bellairs and Jenkin 1960). In some groups of birds, such as loons and grebes, the hypapophyses may be large and elaborate, and they may extend well into the cervical region (Zusi and Storer 1969). However, in other birds, such as *Apteryx*, the hypapophyses are comparatively simple, feebly developed, and they are confined to the anterior few trunk vertebrae as in deinonychosaurs (pers. obs.).

71) Modifications associated with transition point begin close to base of tail. As argued above, Tetanurae is apomorphic compared to Theropoda ancestrally in that the modifications associated with the transition point are more marked. Compared to *Compsognathus* (Ostrom 1978) and Ornithomimidae (Fig. 2E), however, the transition point is more proximally placed in that the transition takes place between caudals 7 and 11 in Deinonychosauria (Fig. 2G) and Avialae (Fig. 2F). Fairly complete caudal series are known from both *Deinonychus* (Ostrom 1969*b*) and the Eichstätt *Archaeopteryx** and they differ from the tails of ornithomimids and other theropods in several ways. First, the neural spines and transverse processes are confined to the first seven to nine vertebrae, although like other archosaurs both structures are more prominent in the larger *Deinonychus* compared to the smaller *Archaeopteryx**. Second, the first 5 caudals have short, boxlike centra and vertically oriented zygapophysial facets. And third, both have modified haemal arches that are longer than deep in lateral view extending nearly to base of the tail. Thus, maniraptorans are the most derived among Theropoda in the development of the dynamic stabilizer tail (Ostrom 1969*b*; Padian 1982). Following Wellnhofer (1974), L. D. Martin (pers. comm.) agrees that long, tapered prezygapophyses are present posteriorly, but argues that only the postzygapophyses are elongate in the anterior portion of the tail in *Archaeopteryx** (Eichstätt). After examining a cast of the specimen in Martin's lab, I have, however, concluded that *Archaeopteryx** had elongate prezygapophyses on caudals beyond those in the base of the tail as in other maniraptorans for two reasons. First, the prezygapophyses in the middle of the tail are variable in length and shape as preserved; if these variations are natural, *Archaeopteryx** would be unlike all other saurians. Second, elongate postzygapophysial articular facets are uniformly present in this region, and this modification seems superfluous without concomitant elongation of the prezygapophyses with which the facets articulate. Taking these factors into account, variation in prezygapophysial shape and length in the midcaudals is here attributed to removal of the counterslab and consequent damage to the narrow and superficial portions of the prezygapophyses.

Although the caudal series is quite modified in Ornithurae, principally by the reduction and fusion of the distal segments and the loss of the zygapophyses, a number of the maniraptoran synapomorphies in tail form have been retained. For example, the short and boxlike centra in the proximal series are widespread among Aves. In addition, although they may be modified and fused to the centra, boat-shaped haemal arches that are longer than deep and flat-bottomed in lateral view are retained in the caudal region of some groups, such as Hesperornithes (Marsh 1880), and loons and penguins (pers. obs.). Like all birds, *Archaeopteryx** has enlarged feathers along the lateral margins of the tail (Ostrom 1976*a*), but then it is the only nonornithurine maniraptoran preserved in an environment of deposition in which feather impressions could be preserved. The orientation of the feathers and caudal zygapophyses in *Archaeopteryx** indicates that the tail was most mobile in the dorsoventral plane, as in dinosaurs generally. Evidently, the horizontal orientation of the tail feathers in extant birds cannot be accounted for in functional terms solely as an adaptation for flight.

72) Coracoid with subrectangular profile. The coracoid is subcircular in profile in Ornithodira ancestrally (see Appendix A). This condition is retained in Sauropodomorpha (Fig. 4B) and Ceratosauria (Raath 1969), and this appears to be the case judging from what remains of the element in *Liliensternus** (Huene

1934). Except for the tapering posteroventral margin (see Part III, character 42), the coracoid is otherwise subcircular in Carnosauria (Madsen 1976) and in the coelurosaurs *Compsognathus* (Ostrom 1978), Ornithomimidae (Fig. 4C), and Caenagnathidae (Barsbold 1983). The coracoid in Deinonychosauria and Avialae is further derived relative to that seen in other Coelurosauria in that it is enlarged, particularly at the ventromedial and posterior margins; these modifications impart to the element a subrectangular profile (Fig. 4E). In addition, a pronounced "coracoid tubercle" lies just anterior to the glenoid rim and immediately ventral to the coracoid foramen. During ontogeny, the shoulder girdle of the chicken transforms from a subrectangular to an elongate coracoid characteristic of Ornithurae; I have been unable to determine if the coracoid was subcircular in outline at its initial stages of development. Interestingly, a subrectangular coracoid has re-evolved *within* Hesperornithes (compare coracoids of *Baptornis* with *Hesperornis* in Martin and Tate 1976) and in some other flightless birds such as the ratites (Feduccia 1980). This appears to be an example of paedomorphosis in that the subrectangular shape is a transitory stage in the transformation of the coracoid in the ontogeny of Aves. This is, however, the terminal stage in the ontogeny of the element in the two successively more remote outgroups of Ornithurae, namely Deinonychosauria and *Archaeopteryx**. Contrary to Tarsitano and Hecht (1980), the coracoid in *Archaeopteryx** is not ancestral with respect to the condition seen in other theropods. On the contrary, the shape and flexure of the element and the enlarged "coracoid tubercle" in *Archaeopteryx** (Fig. 4D) are matched in kind, if not degree, in deinonychosaurs (Fig. 4F) and elmisaurids* (P. J. Currie, pers. comm.). Ostrom (1974*a, b,* 1976*a, b*) and Padian (1982) have explored the significance of the transformations in coracoid morphology and their relationship to the function of the forearm and the origin of flight in the taxa here included in Maniraptora (see also Gauthier and Padian 1985).

73) Elongate forelimb nearly 75% of presacral vertebral column length, and elongate hand nearly equals or exceeds length of foot. As argued above, coelurosaurs are diagnosable in part on the basis of their elongate forelimbs and hands, although the hands of ornithomimids may be secondarily shortened. According to Ostrom (1976*a*), the forelimbs of *Ornitholestes** and Deinonychosauria are about 75% of the length of the presacral vertebral column, and those of *Archaeopteryx** are 120% to 140% of the presacral column length. Moreover, the hand is 92% of the length of the foot in Deinonychosauria (Ostrom 1969*b,* 1976*a*) and the hand exceeds the length of the foot in Avialae ancestrally (Bellairs and Jenkin 1960). Ostrom (1974*b,* 1976*a*), Padian (1982), and Gauthier and Padian (1985) have noted the synapomorphic resemblance between the forelimbs of deinonychosaurs and birds, and have explored the significance of these characters in the origin of flight within Coelurosauria.

74) Ulna bowed posteriorly. As in Archosauria ancestrally, the posterior margin is roughly straight and the element is not bowed posteriorly in Sauropodomorpha (Cooper 1981*a:* 736, fig. 31D), *Procompsognathus** (Ostrom 1981), *Liliensternus** (Huene 1934), Ceratosauria (Welles 1984), Carnosauria (Madsen 1976:137, fig. 42D), and *Compsognathus* (Ostrom 1978). The ulna is only slightly bowed in Ornithomimidae (Osmolska et al. 1972). In contrast, the ulna is strongly bowed posteriorly in Caenagnathidae (Osborn 1924*b*), *Microvenator** (Ostrom 1970), troodontid (Russell 1969:603, fig. 9A) and dromaeosaur (Ostrom 1969*b:* 95, fig. 58A) deinonychosaurs, and *Archaeopteryx** (Ostrom 1976*a*). The ulna is even more prominently bowed in Ornithurae (Bellairs and Jenkin 1960). This apomorphy arose convergently within Pterosauria (Wellnhofer 1978).

75) Semilunate carpal. As argued above, distal carpal I caps the bases of metacarpals I and II in Theropoda ancestrally (Fig. 4K), and this condition is retained in Carnosauria ancestrally (Fig. 4L). The carpus in Ornithomimidae (Osborn 1917) and Tyrannosauridae (Barsbold 1983) is composed of small, poorly formed carpals lacking articular facets, and both taxa appear to be paedomorphic in this respect. Although it is clear that the tyrannosaurid condition derived from the ancestral condition, retained by other carnosaurs such as *Allosaurus,* the condition from which the ornithomimid hand derived is unclear. As in tyrannosaurids, the paedomorphic carpals of ornithomimids could have derived from the ancestral condition. However, because ornithomimids are closer to maniraptorans than carnosaurs are, it is also possible that the paedomorphic carpals could have derived from the condition here considered diagnostic of Maniraptora. I consider the former case to be correct, although I recognize that more information is needed to dispel the ambiguity regarding this point; in any case, this decision has no influence on the final outcome of the analysis.

In contrast to the ancestral theropod condition retained by the tetanurine ancestor, distal carpal I in Maniraptora was transformed into a depressed, semilunate-shaped carpal with a deep, horizontal groove proximally for reception of a reciprocally shaped ridge for articulation with the proximal carpal, and two prominent fossa distally for reception of the bases of metacarpals I and II (see Russell 1969; Ostrom 1976*a*). A semilunate carpal is present in *Coelurus** (Ostrom 1976*a*), Caenagnathidae (Barsbold 1983), Deinonychosauria (Fig. 4N), and Avialae (Fig. 4O). The integration of manal digits I and II in the wrist was initiated in Saurischia ancestrally. Functional integration was further advanced in Theropoda when distal carpal I capped both metacarpals. With the development of a semilunate carpal, the carpus reached a kind of functional equivalence with that of Ornithurae in ancestral Maniraptora. As noted by Russell (1969) and Ostrom (1969*b*), the resulting mesocarpal joint permitted increased mediolateral excursion of the hand relative to the forearm (=190°), a prerequisite to the development of avian powered flight (J. Rayner, pers. comm.).

76) Metacarpal III bowed laterally and very thin compared to metacarpal II. Metacarpal III is neither very thin nor bowed in Sauropodomorpha (Fig. 4I, J), Ceratosauria (Fig. 4K), and Ornithomimidae (Fig. 4M). The third digit and its metacarpal are reduced, but never bowed, in Carnosauria (Fig. 4L). In contrast, metacarpal III is very thin compared to metacarpal II, and it is bowed laterally in Deinonychosauria (Fig. 4N), *Archaeopteryx** (4O; based on pers. obs. of Eichstätt specimen) and most Ornithurae (Bellairs and Jenkin 1960). A gracile third metacarpal is also present in *Ornitholestes** (Osborn 1917) and Caenagnathidae (Osborn 1924*b*). I am unable to determine from the published figures if the element is bowed, and examination of the specimens will be necessary to decide if a thin and a bowed third metacarpal are one and the same character. As in all tetanurines, the third metacarpal lies ventral to the level of second, and the bowed nature of the third metacarpal may only

be apparent in dorsal or ventral view; thus, the preserved orientation of the element is critical in recognizing this character. Differences in orientation as preserved may account for why the third metacarpal of the Berlin *Archaeopteryx** appears bowed in the left hand but not in the right.

77) Posterodorsal margin of ilium curves ventrally in lateral view. The dorsal margin of the ilium is gently arched in profile in Saurischia ancestrally (Fig. 5B, C), although very early in sauropodomorph phylogeny the arching becomes more prominent. The gentle dorsal arc is retained in Theropoda, however, the posterior margin of the ilium is truncated vertically in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), and Ornithomimidae (Fig. 5E). In contrast, the dorsal margin of the ilium curves posteroventrally in profile in Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), Deinonychosauria (Fig. 5F, G), and Avialae (Fig. 5H, I).

78) Pubic peduncle of ilium extends ventrally beyond level of ischiadic peduncle, and pubis directed posteroventrally. The pubic and ischiadic peduncles terminate at about the same level and the pubis points anteroventrally in Sauropodomorpha ancestrally (Fig. 5B). The ancestral condition is retained in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), *Ornitholestes** (Osborn 1917), and Ornithomimidae (Fig. 5E). In contrast, the pubic peduncle extends further ventrally and the pubis is directed more or less posteroventrally in Deinonychosauria (Fig. 5F, G) and Avialae (Fig. 5H, I). Ostrom (1976*b*) was the first to note that both the morphology of the pubic peduncle of the ilium and the preserved orientation of the pubis in *Deinonychus* indicated that the pubis could not have projected anteroventrally as in dinosaurs ancestrally. This observation has been corroborated by finds of articulated dromaeosaur pelves (Barsbold 1977, 1979, 1983; Barsbold and Perle 1979). Of course, in the absence of articulated pelves the precise orientation of the pubis is difficult to determine, as the variety of restorations of pubic orientations in *Archaeopteryx** and dromaeosaurs graphically illustrates (Fig. 5F, G). Tarsitano and Hecht (1980) argued that Ostrom's (1976*a*) restoration of the *Archaeopteryx** pelvis was incorrect, and that the pubes of *Archaeopteryx** were in fact oriented more as in Ornithurae. Regardless of the degree of reversal, however, the point to be emphasized is that Deinonychosauria and Avialae are like one another and unlike all other Theropoda in the great length of the pubic peduncle and that the pubis no longer points anteroventrally. If *Archaeopteryx** is in fact more birdlike in this respect than other theropods, that is consistent with our belief that it is a bird, but this observation has no bearing on the question of relationship between birds and deinonychosaurs.

Troodontids present a potentially more serious problem when trying to optimize the character "reversed pubis" on the most parsimonious tree for all the data. That is to say, an outline drawing of a pelvis said to be from *Saurornithoides* first appeared in Barsbold (1977), and the pubis was figured in the unreversed, ancestral condition. Subsequently, dashed lines included in another outline drawing of the same pelvis in Barsbold (1983) revealed that both drawings represented an incomplete specimen. A formal description of this specimen, including adequate illustrations and rationale for its referral to *Saurornithoides,* has yet to be published. If the ancestral form of the pubis and its attachment to the ilium can be verified in Troodontidae, then one might question the monophyly of Deinonychosauria, which would require independent origins (i.e., convergence) to explain the similarities between the raptorial second pedal digits and didactyl pes in troodontids and dromaeosaurs. Alternatively, if one accepts the raptorial second pedal digit and didactyl pes of Deinonychosauria as synapomorphic, then reversal of the pubis took place twice among maniraptorans: once in dromaeosaurs and once in avialans. Yet another and equally parsimonious hypothesis would be the appearance of the reversed pubis in ancestral Maniraptora, with its subsequent reversal to the ancestral condition in troodontids; once again one must assume that troodontids are most closely related to dromaeosaurs on the basis of shared apomorphies in the raptorial second pedal digit and didactyl pes.

Each of these interpretations requires three evolutionary events to account for the distribution of these two characters among these three taxa. There is thus no basis for choice among the possible alternatives. Accordingly, until there is firmer evidence to the contrary, I will consider the pubis to have been reversed in the immediate common ancestor of deinonychosaurs and birds. Assuming this to have been the case, a reversed and posteroventrally oriented pubis must have arisen three times within Ornithosuchia, because this condition also obtains in Ornithischia (Fig. 5A) and segnosaurs (Barsbold and Perle 1979; Barsbold 1983; segnosaurs are here considered sauropodomorph dinosaurs of uncertain relationships, see Appendix A).

79) Pubic foot reduced anteriorly. As noted above, a pubic foot is present in Tetanurae ancestrally. However, it is expanded both fore and aft in Carnosauria (Fig. 5D), Caenagnathidae (Barsbold 1983), and Ornithomimidae (Fig. 5E). In contrast, the pubic foot is much less developed anteriorly than it is posteriorly in *Compsognathus* (Ostrom 1978), *Microvenator** (Ostrom 1970), *Coelurus** (Marsh 1896), Deinonychosauria (Fig. 5F, G), and *Archaeopteryx** (Fig. 5H; Padian 1982). The absence of a pubic foot in Ornithurae is considered a secondary modification (Fig. 5I). This character, like the preceding one and the following two characters, has yet to be determined in troodontids. The condition of the pubic foot in caenagnathids presents certain problems; the profile of the structure differs in each of Barsbold's figures (e.g., 1979, 1983), but it is usually portrayed as being longer anteriorly than posteriorly. In light of the evidence under consideration, caenagnathids are part of Maniraptora; thus their pubic foot must have been modified from the anteriorly abbreviated condition seen in other maniraptorans. This may, however, simply reflect inaccuracies in Barsbold's reconstructions.

80) Ischium two-thirds or less of pubis length. The ischium is at least three-quarters of the length of the pubis in Sauropodomorpha ancestrally (Fig. 5B), as it is in *Liliensternus** (Huene 1934), Ceratosauria (Fig. 5C), Carnosauria (Fig. 5D), and Ornithomimidae (Fig. 5E). In contrast, the ischium is no more than two-thirds of the length of the pubis in *Compsognathus* (Ostrom 1978) and Caenagnathidae (Barsbold 1983), and although the pubis is incomplete distally, this appears to be the case in *Ornitholestes** as well. As noted by Ostrom (1976*a, b*) and Padian (1982), the ischium is only half or less of the pubic length in Deinonychosauria (Fig. 5F, G) and *Archaeopteryx** (Fig. 5H). Ornithurae is hypothesized to be secondarily modified owing to reduction in the length of the pubis (Fig. 5I).

81) Obturator process distally placed on ischium. As argued

above, an obturator process on the ischium is the ancestral condition for Tetanurae. In Carnosauria the process is proximally placed (Fig. 5D), and this condition is retained in Ornithomimidae (Fig. 5E). *Ornitholestes** (Osborn 1917) appears to have a large and distally placed obturator process but its pelvis is not well enough preserved to allow further interpretation. The obturator process is distally placed in *Compsognathus* (Ostrom 1978) and Caenagnathidae (Barsbold 1983), and it is both enlarged and distally placed in Deinonychosauria (Fig. 5F, G). As discussed above, the condition in *Archaeopteryx** is difficult to interpret; either an obturator process is absent, or it is represented by the ventral of the two processes at the distal end of the ischium (Fig. 5H). This process is absent in Ornithurae, but in any case its absence in birds is here hypothesized to represent a phylogenetic loss rather than retention of an ancestral condition.

82) Anterior trochanter nearly confluent with proximal head of femur. As noted above, the anterior (=lesser) trochanter is a tall flange that is separated by a deep cleft from the femoral shaft in Carnosauria (Madsen 1976) and Coelurosauria ancestrally. Ornithomimidae (Osmolska et al. 1972) and *Microvenator** (Ostrom 1970) retain the ancestral tetanurine condition. The femoral head in Deinonychosauria (Ostrom 1976*b*) and *Archaeopteryx** (Ostrom 1976*a*) is like that of other coelurosaurs in that the anterior trochanter extends to the femoral head (Padian 1982). However, maniraptorans are distinguished from other coelurosaurs in that the anterior trochanter is separated from the femoral head by no more than a shallow groove, and the anterior trochanter is thus nearly to completely confluent with the femoral head. Ostrom (1976*a*:124, 125) described and figured the proximal end of the femur of *Microvenator**, *Archaeopteryx**, and *Cathartes*, and argued that the femur of *Archaeopteryx** is intermediate between that of "theropods" and Recent birds, in which there is no separate anterior trochanter (except as an occasional variant among neognaths). As is evident from Romer (1927), birds recapitulate the phylogenetic history of this transformation during ontogeny; the *pifi 2* attaches in the ancestral archosaurian position and subsequently migrates proximally through various theropod attachment points, eventually arriving at the position seen in extant birds. Thus, the five (or four) muscles inserting on the avian major trochanter yield a composite anterior plus greater trochanter (T. Rowe, pers. comm.).

83) Absence of fourth trochanter on femur. Tarsitano and Hecht (1980) noted that *Archaeopteryx** and other nonswimming birds are unusual among archosaurs in the loss of the fourth trochanter. As noted above, however, the fourth trochanter is feebly developed among coelurosaurs ancestrally, and it is absent in Deinonychosauria and birds. Pterosaurs also lost the fourth trochanter (Wellnhofer 1978), and this area of muscle attachment is also reduced in a number of very large quadrupedal dinosaurs, such as Sauropoda (see Appendix A).

84) Pedal digit IV longer than II and closer to III in length. Pedal digit IV is longer than II and closer to III in length in archosaurs ancestrally (Fig. 6J–N). As argued above, however, theropods are apomorphic in that pedal digit II is only a little shorter than IV, and the foot is thus more symmetrically developed about digit III (Fig. 6O). The symmetrical theropod foot is retained in *Procompsognathus** (Ostrom 1981), Ceratosauria (Raath 1969), Carnosauria (Madsen 1976), and Ornithomimidae (Osmolska et al. 1972). However, the ancestral theropod condition appears to have reversed within Coelurosauria in that pedal digit IV approaches III in length, and thus is longer than digit II in *Ornitholestes** (Ostrom 1969*b*), *Compsognathus* (Ostrom 1978), Caenagnathidae (Barsbold 1983), Deinonychosauria (Russell 1969; Ostrom 1969*b*), and Avialae (Fig. 6P). Tarsitano and Hecht (1980) argued that birds were plesiomorphic compared to other theropods owing to the greater length of pedal digit IV. However, in view of the data presented here, this character is hypothesized to be an apomorphic reversal rather than a plesiomorphic retention in birds and other maniraptoran theropods.

Another aspect of the construction of the pes that may be related functionally to a lengthened fourth digit is the development of a raptorial second pedal digit, an attribute that is taken to extreme in troodontids and dromaeosaurs. No other theropods aside from cariamid neognaths approach the degree of specialization characteristic of deinonychosaurs. However, a few other extinct maniraptoran coelurosaurs appear to show incipient specializations to this end. For example, an enlarged articular surface indicating a greater radius of excursion between the second and third phalanx in the second pedal digit is apparent in *Elmisaurus** (Osmolska 1981) and *Ornitholestes** (Osborn 1917); unfortunately, the more distal portion of this digit, including the ungual, were not preserved in either specimen. As pointed out by D. Yalden (pers. comm.), the claw impressions encasing the pedal unguals of *Archaeopteryx** resemble the claws of arboreal mammals more than they do the claws of raptors using the foot to secure prey. The claw impressions of *Archaeopteryx** are also unlike those of *Compsognathus*, in that the impressions of the latter display a flat-bottomed shape that would have been better suited to running than climbing. Yalden's evidence is compelling; nevertheless, *Archaeopteryx** clearly has an enlarged articular surface on the distal end of the first phalanx of the second digit (pers. obs. of Eichstätt specimen), accompanied by an enlarged claw (Wellnhofer 1974). This indicates that *Archaeopteryx** possessed some ability to pin and secure prey with its foot (or use this toe as a defensive weapon), and this attribute may have been present in maniraptorans ancestrally. To be sure, none of these specimens is as specialized as are deinonychosaurs in this respect. Nonetheless, the foot of *Archaeopteryx** appears to be intermediate between the functionally tridactyl foot of theropods ancestrally and the functionally didactyl and raptorial foot of deinonychosaurs.

If the use of the foot to grasp prey is ancestral for maniraptorans, it might explain the initial advantage of a reversed first digit (the hallux), especially in an organism whose formerly raptorial forelimbs had been preempted to serve the demands of powered flight. Because the hallux opposes the action of the second digit, the pincerlike action of both digits would have enhanced the ability to grasp with the foot. This interpretation need not contradict Yalden's conclusions regarding the use of the feet in *Archaeopteryx**. By the stage of avian evolution represented by *Archaeopteryx**, the pes may have played a critical role in its ability to climb. However, the ability to grasp with the pes, so necessary to an arboreal biped, may simply have been inherited from a more distant and nonavialan ancestor. As noted above, a lengthened fourth toe is common among extant birds. However, aside from the deinonychosaurlike pes of cariamids, I am not aware of any other ornithurine bird that

has a similarly modified second pedal digit (although a number of ratites are nonetheless able to inflict severe damage with this toe; Ostrom 1969*b*). Accordingly, this attribute is considered to have been lost in Ornithurae ancestrally, and to have re-evolved in the common ancestor of cariamid neognaths.

Conclusions

I. Summary of the Main Phylogenetic Conclusions of this Work

As implied by their name "lizard-hipped" dinosaurs, saurischians have always been grouped on the basis of their plesiomorphic resemblances. However, compared to alternative hypotheses, such as monophyly of Ornithischia-Sauropodomorpha or Ornithischia-Theropoda, the taxon Saurischia provides a better summary of the evidence pertinent to hypotheses of monophyly. Accordingly, Saurischia is herein defined ostensively to include birds and all dinosaurs that share a more recent common ancestor with birds than they do with Ornithischia. The most obvious of the ten synapomorphies uniting Saurischia is their elongate, mobile, and S-shaped necks, a character that distinguishes birds among extant amniotes. Other birdlike attributes present in the ancestral saurischian include a variety of modifications of the manus, such as digit II being the main axis of the hand, a uniquely modified pollex, the palmar displacement of the lateral digits, and the relatively large size of the hand. To these may be added other synapomorphies in the skull and postcranial skeleton, such as the modification of the premaxilla, the spread onto the frontals of the area of origin of the temporal musculature, the modification of the atlanto-axial joint, the development of cervical epipophyses, and the presence of hyposphene-hypantra accessory intervertebral articulations.

Saurischia is composed of two principal lineages, the extinct Sauropodomorpha and extant Theropoda. Twenty-five synapomorphies unite Theropoda within Saurischia. Intact skulls are known from few extinct theropods, and the only synapomorphies so far identified from this region of the skeleton are the characteristically modified vomers and intramandibular joint. The vomers in Ratitae and Tinami are little changed from the ancestral condition in theropods. Most extant birds retain the basic theropod shape of the dentary-postdentary articulation and some degree of intramandibular mobility, although they are unlike theropods ancestrally in that they possess a fused mandibular symphysis. Intramandibular mobility has been lost in birds that have short, powerful jaws with broad mandibular symphyses. From the perspective of the ancestral condition in Theropoda, these birds invariably have unusual diets. Most theropod synapomorphies are derived from the more completely known postcranial skeleton. The ancestral theropod was well suited to cursorial habits and was distinctively birdlike, as is indicated by a light, hollow skeleton, a broader area of origin of muscles arising from the ilium, a variety of modifications of the hindlimbs and feet, and a tail that was thinned and stiffened distally to enhance its role as a dynamic stabilizer. The ancestral theropod retained the carnivorous habits ancestral for Archosauria, but its raptorial hands indicate further specialization toward this end. Moreover, the intramandibular joint suggests macropredaceous habits in that it would enable theropods to ingest relatively larger prey.

The late Triassic *Procompsognathus** and *Halticosaurus** are of uncertain relationships, and they are therefore placed *incertae sedis* within Theropoda. Among the early theropods are several taxa, including the well-represented *Coelophysis, Syntarsus,* and *Ceratosaurus,* that are included here in a modified version of Marsh's Ceratosauria. As constituted here, Ceratosauria is the sister-group of a new taxon, Tetanurae, which includes birds and all theropods that are closer to birds than they are to either Ceratosauria or to the other early theropods. The monophyly of Tetanurae is supported by 17 synapomorphies, including a profound difference between the larger, mobile proximal and the narrow, stiffened distal parts of the tail. Other birdlike attributes of Tetanurae include the presence of a large maxillary fenestra, antorbital tooth row, loss of dentary caniniform tooth, spine tables in the anterior cervicals, enlarged hand, basal appression of metacarpals I and II, palmar displacement of metacarpal III, loss of manal digit IV beyond embryonic stages of development, pubic foot, enlarged ascending process, and shortened metatarsal I.

Coelurosauria is ostensively defined to include birds and all theropods that are closer to birds than they are to carnosaurs. Coelurosauria is thus removed from its classical and paraphyletic status; and in keeping with evolutionary theory, Coelurosauria is applied instead to a monophyletic taxon encompassing *Ornitholestes**, *Coelurus**, *Compsognathus*, *Microvenator**, *Saurornitholestes**, *Hulsanpes,* Elmisauridae*, Caenagnathidae, Ornithomimidae, Deinonychosauria, Avialae, and their immediate common ancestor. Fifteen synapomorphies distinguish Ornithomimidae, Deinonychosauria, and birds from Carnosauria, and at least some of these apomorphies are shared by the remaining coelurosaurs listed above. Several characters distinguishing extant birds among archosaurs are seen in the skull and hindlimb of all coelurosaurs, but from the standpoint of powered flight, the most interesting of these are the modifications of the forelimb and pectoral girdle. These modifications, normally thought to be related to powered flight, include a fused and bony sternum, furcula, elongate forelimb and hand, and the beginnings of medial enlargement of the coracoid.

A new taxon, Maniraptora, is proposed for the group of theropods including birds and all coelurosaurs that are closer to birds than they are to Ornithomimidae. The immediate common ancestor of birds and deinonychosaurs may be distinguished from ornithomimids by possession of 17 synapomorphies. Even nonavian maniraptorans are essentially birdlike in many details of their morphology, including reduction (or loss) of the prefrontal, stiffening and thinning of all but the proximal part of the tail, a characteristically modified coracoid, very long forelimb, bowed ulna and third metacarpal, several modifications of the pelvis including a reversed pubis (at least in dromaeosaurs and birds), absence of discrete fourth and anterior trochanters on the femur, birdlike proportions of the relative lengths of pedal digits II, III, and IV, and at least the incipient development of a raptorial second pedal digit. Various specializations indicate that the raptorial function of theropod forelimbs reached its apex in ancestral maniraptorans. These modifications played an important role in the origin of flight, because the essential elements of the flight stroke are realized in the manner of folding and unfolding the hands, and extending and retracting the forelimbs and hands during prey capture (Padian 1982; Gauthier and Padian 1985).

The precise diagnosis and contents of Maniraptora are prob-

lematic. *Compsognathus* presents particular difficulties; it shares maniraptoran characters 79, 80, 81, and 84 that are absent in ornithomimids, but it retains the ancestral condition, an unbowed ulna, indicating that caenagnathids, *Microvenator**, deinonychosaurs, and birds are more closely related to one another than any of them is to *Compsognathus*. The anomalously short forelimbs of *Compsognathus* present further problems; the hand in particular is incomplete and after examining the specimen I do not feel secure with Ostrom's (1978) conclusions regarding the number of digits. Also, the ornithomimid tail appears in some ways more maniraptoranlike than is that of *Compsognathus*. Thus, it appears that *Compsognathus* is outside the remaining maniraptorans, and it is also possible that it is outside a possible ornithomimid-maniraptoran group.

Caenagnathidae, *Coelurus**, *Microvenator**, Elmisauridae*, and *Saurornitholestes**, and especially *Ornitholestes**, are closer to birds and deinonychosaurs than are ornithomimids. Although this conclusion seems secure, these taxa are so incompletely known that the details of their phylogenetic relationships remain obscure. Accordingly, these taxa are placed *incertae sedis* within Maniraptora, and with some reservations, *Compsognathus* is also included in this taxon. Compared to *Compsognathus*, it is clear that deinonychosaurs and birds are more closely related in that they share characters 69, 71, 72, and 78, but because of incomplete data it is not clear when these attributes arose within Maniraptora. The distinctly birdlike pelvis of dromaeosaurs appears to be absent in most other maniraptorans, thus indicating that this character arose within the group. If, as Barsbold (1983) suggests, these modifications are absent in troodontids, then the monophyly of Deinonychosauria would be brought into question; in any case, the precise level at which these modifications arose is at present indeterminable. Future discoveries and reanalyses will decide which among the 17 synapomorphies listed for Maniraptora are diagnostic of all, as opposed to some, members of this group. The cladograms in Figures 8 and 9 depict the phylogenetic relationships among Theropoda proposed here.

II. The Problem of the Definition of the Name Aves

Aves was initially applied to extant birds alone (Linne 1758). Subsequent finds of other feathered theropods from outside the immediate ancestry of all extant birds (i.e., *Archaeopteryx**, Hesperornithes) resulted in the term Aves being applied to a more inclusive taxon. Although this decision accurately reflects phylogenetic relationships, it also has the unfortunate side effect of diminishing the phylogenetic informativeness and stability of the name Aves. That is to say, Aves currently summarizes only those synapomorphies diagnostic of what I call Avialae, because it restricts the diagnosis of Aves to those characters that are determinable in the fossil *Archaeopteryx**.

An example of the kind of problem that this decision has generated is evident in Wellnhofer and Whetstone's disagreement over the identity of a particular bone in *Archaeopteryx**. Wellnhofer (1974) considered the element in question a squamosal, whereas Whetstone (1983) claimed it to be an opisthotic; surely, neither would have difficulty identifying these elements in the skulls of extant birds. This raises the issue of whether or not such an easily recognizable taxon as extant Aves should be left to the vagaries too often inherent in interpreting the morphology of fossils. One must bear in mind that all synapomorphies present in *Archaeopteryx** must also be present in extant birds, although perhaps in a modified form. However, the reverse cannot be the case; not only do extant birds share a more recent common ancestor with one another than any of them does with *Archaeopteryx**, but extant birds share numerous apomorphies that are not preservable in fossils. Furthermore, it is exceedingly unlikely that any fossil would lead to the conclusion that Recent birds are not most closely related to each other among extant amniotes. After all, Appendix A and the text above record over 100 synapomorphies that distinguish the skeletons of extant birds from their nearest living relatives, the crocodiles; and there are numerous characters in soft anatomy, behavior, physiology, and biochemistry that are diagnostic of this taxon as well.

Another drawback of current practice is that it treats characters as if they were defining, in the sense that if an organism has feathers, it must be a bird. Not only is this perspective typological and thus antievolutionary, but one can envision the difficulties resulting from the possible discovery of feathers in deinonychosaurs, which most certainly did not fly. Moreover, under current practice how would one classify a group of birds that lost feathers during their evolution? In the phylogenetic system, this presents no problem, for if an organism is born to a bird, it is a bird, regardless of the characters it may or may not possess. Characters may aid recognition of ancestry, but they do not define it (Gauthier et al., in prep.). Accordingly, it is recommended that the taxon Aves be standardized in the phylogenetic system by applying this name only to that portion of Theropoda that includes the most recent common ancestor of Ratitae, Tinami, and Neognathae, and all of its descendants.

To reflect the more complex relationships that are of interest mainly to paleontologists, new or less widely used names are applied to taxa including Aves and one or more of its extinct sister-groups. The name Ornithurae is applied to Aves plus all extinct maniraptorans that are closer to Aves than is *Archaeopteryx**, and the name Avialae is applied to Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria. Thus, although the meaning of Avialae and Ornithurae is expected to vary according to the discovery of new fossils, the contents and diagnosis of the taxon Aves in the context of extant amniotes will remain unchanged.

Birds are poor candidates for fossilization and the paucity of their fossil record is widely recognized. This unfortunate circumstance is not confined to birds alone, but applies to Theropoda generally, all of which have lightly constructed skeletons for their size. Nevertheless, theropod stratigraphic occurrences are concordant with the phylogenetic hypothesis offered here. For example, Ceratosauria first appears in the late Triassic, although most ceratosaurs are reported from the early Jurassic, and they persist until the late Jurassic. Continental deposits of mid-Jurassic age are rare, so it is not until the late Jurassic that theropods once again become relatively common in the fossil record. By the late Jurassic most of the major tetanurine lineages have appeared: carnosaurs, ornithomimids, and maniraptorans, including birds, are reported from Upper Jurassic sediments. Indeed, the only major coelurosaur lineage that is not yet represented in the late Jurassic is Deinonychosauria, whose earliest appearance in the fossil record is in the early Cretaceous. Or-

nithurines are also reported from the early Cretaceous, and the earliest record of Aves is in the late Cretaceous.

III. Implications for the Origin of Flight

The above-hypothesized relationships among Theropoda have important implications for hypotheses concerning the origin of flight. Most of the skeletal modifications enabling *Archaeopteryx** to fly are present in all maniraptorans, although only avialans are able to fly. This requires that any functional explanation for the origin of flight must also account for the apomorphic similarities shared by *Archaeopteryx** and coelurosaurs in general and deinonychosaurs in particular (Gauthier and Padian 1985). One may not agree with the particular explanation initially offered by Ostrom (1974*a*, i.e., the insect net hypothesis), but one must appreciate that insofar as he sought to develop a general explanation for the function of the forelimbs and pectoral girdle in Maniraptora, his approach was basically sound. Those who favor other hypotheses should begin to analyze the evolution of flight in theropods in the context of the independent line of evidence afforded by their phylogenetic history (Gauthier and Padian 1985).

In view of the evidence placing birds within Maniraptora, Coelurosauria, Tetanurae, Theropoda, Saurischia, Dinosauria, Ornithodira, Ornithosuchia, and Archosauria, it should be clear that birds are neither the sister-group of mammals (Gardiner 1982), nor are they the sister-group of crocodiles (Walker 1972; Martin 1983*a*). Likewise, this evidence provides a new perspective on Walker's (1964) suggestion that theropods are polyphyletic. Walker's hypothesis can be rejected on two counts: (1) *Ornithosuchus* is not a carnosaur, and (2) the alternative hypothesis of separate origins of "carnosaurs" and "coelurosaurs" from within "thecodonts" is uninformative, because it claims no more than that "carnosaurs" and "coelurosaurs" are archosaurs. A similar line of reasoning can be applied to Chatterjee's (1985) postulated connection between the poposaurid rauisuchian pseudosuchian *Postosuchus* and tyrannosaurid carnosaurs; in the context of all the evidence, their shared apomorphic resemblances beyond those common to all archosaurs must be considered convergent.

A popular misconception is that all dinosaurs were huge lumbering beasts that long ago became extinct. To be sure, only one lineage of dinosaurs survived the end of the Cretaceous. Nevertheless, this lineage currently accounts for nearly half of the total species diversity of extant Amniota. Birds are living dinosaurs, and as such they have extended the preeminence of Dinosauria among terrestrial vertebrates from the late Triassic to the present day.

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Appendix A

Archosaur Phylogeny: On the Relationships of Certain Extinct Archosaurs to Extant Crocodiles and Birds

The hypotheses of relationship discussed below derive mainly from Gauthier (1984 and references therein). They provide the context in which the present analysis of saurischian phylogeny was undertaken. As used here, Sauria, n. comb., is restricted to the least inclusive taxon encompassing extant diapsids, and the name Diapsida is applied to the taxon including extant Sauria and its extinct sister-group, Araeoscelidia. The more inclusive groups of Recent Amniota recognized in this work follow the usage in Gauthier (1984) and Gauthier et al. (in prep.): Mammalia is the sister-group of Reptilia within Amniota; Reptilia includes the sister-taxa Chelonia and Sauria; and Sauria includes the sister-taxa Lepidosauria and Archosauria.

Archosauria (n. comb.) is redefined to encompass all the descendants of the most recent common ancestor of crocodiles and birds. So defined, some taxa previously included within Archosauria are now excluded from it. Thus, Proterochampsidae, Erythrosuchidae, and Proterosuchidae are here considered successively more remotely related outgroups of Archosauria (s.s.), rather than "proterosuchian-grade archosaurs." Defining Archosauria in this way provides a more fruitful perspective from which to examine archosaur phylogeny. Rather than proceeding from a position of less evidence—by trying to determine which group of "thecodonts" gave rise to birds or crocodiles—we may now regard more precisely stated hypotheses from the position afforded by more secure knowledge (i.e., no one has ever confused a living crocodile with a living bird). That is to say, by defining Archosauria and its major subgroups on the basis of the ancestry of extant archosaurs, an extinct and diagnosible archosaur can have only one of two possible relationships; it could be more closely related to birds, or it could be more closely related to crocodiles. Pseudosuchia (n. comb.) is redefined to include extant crocodiles and all extinct archosaurs that are closer to crocodiles than they are to birds. Likewise, Ornithosuchia (n. comb.) is redefined to include extant birds and all extinct archosaurs that are closer to birds than they are to crocodiles.

I realize that it is not enough simply to list supposed "synapomorphies" in support of a particular hypothesis. To make the hypothesis most vulnerable to test, one should proceed through the entire system of Hennigian argumentation for each character and array this evidence in a taxon/character matrix. Furthermore, I have had to consider many specimens of taxa that I have not had the opportunity to study first-hand, and I have relied instead on published illustrations and descriptions. Finally, I have not had the time to consider several recent publications on archosaur phylogeny (e.g., Paul 1984*a*, *b*) in the detail that they deserve. Accordingly, the following can only be considered a preliminary analysis (or as R. Bakker [pers. comm.] put it, an exercise in "armchair cladistics"). To balance these caveats, I should add that the hypothesis presented below is broadly concordant with those arrived at by other workers in this area (e.g., Benton 1985; Parrish 1984 and pers. comm.).

As defined here, Pseudosuchia and its major subgroups can be diagnosed as follows (cases of homoplasy will only be listed if they occur between, rather than within, basic taxa).

Pseudosuchia

(n. comb. =Parasuchia, Aetosauria, Rauisuchia, and Crocodylomorpha—including crocodiles)

1) Crocodile-normal crurotarsal ankle joint, in which the peg is on the astragalus and the socket is on the calcaneum.
2) Calcanear tubercle enlarged (also in Ornithosuchidae).
3) Cervical ribs short and stout.
4) Discrete postparietal confined to early juvenile or prehatching ontogenetic stages (also in ornithosuchians aside from *Euparkeria**—see discussion below).
5) Palatal teeth absent (also in ornithosuchians aside from *Euparkeria**).

Unnamed Taxon Including Aetosauria, Rauisuchia, and Crocodylomorpha

6) Septomaxilla absent.
7) No separate postparietal at any time in posthatching ontogeny.
8) Fusion of second intercentrum and first centrum in juvenile or earlier stages of ontogeny.
9) Triradiate pelvis (also in ornithosuchians; see Parrish 1984).
10) "Screw-joint" tibio-astragalar articulation (R. Long, pers. comm.; also in Ornithosuchidae, M. Parrish, pers. comm.).
11) Fully developed crocodile-normal crurotarsal joint (Krebs 1963; Brinkman 1981).
12) Osteoderms on ventral surface of tail.

Unnamed Taxon Including Rauisuchia and Crocodylomorpha

13) First (atlantal) intercentrum much longer than wide.
14) Axial diapophysis reduced or absent (or corresponding process of axial rib reduced; J. Clark, pers. comm.).
15) Enlarged, pneumatic, basipterygoid processes (J. Zawiskie, pers. comm.).
16) Length of pubis exceeds three times width of acetabulum (also in ornithosuchians aside from *Euparkeria**).
17) Fewer than four phalanges in pedal digit five.

Crocodylomorpha

18) Quadratojugal extends to dorsal surface of skull.
19) Quadrate and quadratojugal inclined anterodorsally.
20) Quadrate contacts prootic.
21) Postfrontal absent (also in ornithosuchians aside from *Euparkeria** and Ornithosuchidae).
22) Maxillaries contact to form secondary palate anteriorly.
23) Internal jugular vein absent.
24) Squamosal without ventral ramus.
25) Post-temporal fenestra very small (analogous modification achieved by separate means within Ornithosuchia).
26) Fenestra "pseudorotunda" present (also appearing at some unknown level within ornithischians and theropods).

27) Entire deltopectoral crest distally placed.
28) Clavicles absent.
29) Coracoid ventromedially elongate (also in pterosaurs).
30) Radiale and ulnare elongate and columnar.
31) Pedal digit five with fewer than four phalanges (also in ornithosuchians).

M. Parrish (pers. comm.) noted some interesting characters indicating a closer relationship between aetosaurs and rauisuchians than is suggested by the characters listed above. Crocodylomorphs may turn out to be the sister-group of a rauisuchian-aetosaur group, or they may be the sister-group of rauisuchians as suggested above. Nevertheless, it must be emphasized that the analyses of Parrish and Gauthier agree on two points: 1) Pseudosuchia is monophyletic, and 2) Parasuchia is the sister-group of the crocodile-aetosaur-rauisuchian group.

Ornithosuchia
(=*Euparkeria**?, Ornithosuchidae, *Lagosuchus**, Pterosauria—including *Scleromochlus**, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda—including birds)

One might question whether or not *Euparkeria** is inside or outside of Archosauria (s.s.). Evidence presented below indicates that *Euparkeria** is closer to birds than to crocodiles. This early Triassic archosaur is, however, exceedingly primitive, and some evidence supports an alternative hypothesis in which Pseudosuchia and Ornithosuchia (excluding *Euparkeria**) are most closely related. For example, unlike *Euparkeria**, all other archosaurs share the apomorphic absence of palatal teeth, absence of discrete intercentra throughout the trunk and in most of the cervical region, and absence of a discrete postparietal and exoccipitals beyond juvenile stages of development. Thus, four potential synapomorphies could unite all archosaurs with respect to *Euparkeria**. However, discrete trunk intercentra are also absent in the two successively more remote outgroups of Archosauria, Proterochampsidae and Erythrosuchidae; the presence of discrete trunk intercentra in *Euparkeria** must then be interpreted as either a reversal, or as further evidence of the immaturity of the known specimens. Six potential synapomorphies unite *Euparkeria** with the birdlike archosaurs. I have been unable to discover any evidence that *Euparkeria** is closer to crocodiles.

Looking again at the evidence, it is interesting to note that intercentra, postparietals, and exoccipitals are present in juvenile archosaurs ancestrally (e.g., Camp 1930; de Beer 1937). That *Euparkeria** could be represented by juvenile or at least incompletely grown specimens is also indicated by unfinished articular surfaces on long bones, an unossified distal tarsal II, an unfused scapulocoracoid, neural arches that are unfused with their respective centra, and separate sacral ribs. Thus, rather than character discordance arising from convergence, the apparent discordance may arise instead from comparing nonequivalent ontogenetic stages. If one disregards the apparently age-related characters, and accepts the evidence indicating that *Euparkeria** is an ornithosuchian archosaur, then one need only invoke a single ad hoc hypothesis of convergence, namely, the independent loss of palatal teeth in Pseudosuchia on the one hand, and in Ornithosuchia aside from *Euparkeria** on the other, to account for the available evidence. This problem should be given further consideration, but for the present the following characters are accepted as diagnostic of Ornithosuchia. Fortunately, *Euparkeria** is so plesiomorphic that its ultimate placement makes little difference in determining character polarity in the following analysis.

1) Squamosal reduced and descending ramus gracile (reversed in large-headed, carnivorous ornithosuchians such as tyrannosaurs).
2) Centra steeply inclined in at least the first four postatlantal cervicals.
3) Modifications in the hindlimb and girdle correlated with semierect gait (also in pseudosuchians aside from Parasuchia; see Parrish 1984).
4) Ventral flange of astragalus absent.
5) Crocodile-reversed ankle joint, with peg on calcaneum and socket on astragalus (including loss of perforating foramen; see Cooper 1980, 1981*b;* Brinkman 1981; Thulborn 1982).
6) Pedal digit five with fewer than four phalanges (also in rauisuchian-crocodylomorph group).

Unnamed Taxon Including Ornithosuchidae, *Lagosuchus, Pterosauria, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda**

This taxon might more profitably be considered Ornithosuchia, in that the distribution of characters among archosaurs leaves little doubt as to the monophyly of this taxon. Until the position of *Euparkeria** is better understood, however, this taxon will remain unnamed. Should *Euparkeria** be shown to be outside of Archosauria (s.s.), then by definition the name Ornithosuchia would be restricted to this taxon. This group of archosaurs is diagnosed by the following synapomorphies (if indeterminable owing to nonpreservation or profound transformation, character will be followed by L? for *Lagosuchus** and Pt? for pterosaurs, including *Scleromochlus**).

7) Discrete postparietal absent in post-hatching ontogeny (L?; also in pseudosuchians).
8) Palatal teeth absent (L?; also in pseudosuchians).
9) Coracoid tubercle lies close to glenoid fossa and coracoid foramen.
10) First metacarpal with offset distal condyles, and pollex directed medially and bearing enlarged ungual (L?;Pt?).
11) Manus more asymmetrical than in pseudosuchians, with inner digits much larger than outer digits (L?;Pt?).
12) Supra-acetabular buttress.
13) Prominently triradiate pelvis, with pubis length at least three times width of acetabulum (also in crocodylomorph-rauisuchian group, and to a lesser extent aetosaurs).
14) Anterior trochanter on femur appears early in posthatching ontogeny.
15) Aliform fourth trochanter (Pt?; characters 13–16 correlated with erect posture; see Parrish 1984).
16) Fifth metatarsal gracile.

Ornithodira (n. txn.)
(Gr. *ornithos,* bird; *deire,* neck)
(=*Lagosuchus**, Pterosauria, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda)

The possession of the following synapomorphies makes it clear that ornithodiran monophyly is one of the most highly corroborated hypotheses in archosaur phylogeny. Indeed, the immediate common ancestor of Ornithodira was fundamentally more birdlike than were ornithosuchids, *Euparkeria**, or pseudosuchians. Unfortunately, the precise level at which the following characters arose is problematic in some instances, because *Lagosuchus** is incompletely known and pterosaurs are so specialized. If a character listed as diagnostic of Ornithodira is only questionably present due to incomplete preservation or profound modification, this fact will be denoted by either (L?) for *Lagosuchus** or (Pt?) for pterosaurs, following the character in question. It is not yet clear if *Lagosuchus** or Pterosauria is the immediate sister-group of dinosaurs, although the femur is, at least in *Dimorphodon,* more dinosaurlike than is that of *Lagosuchus** (Gauthier 1984).

17) Postfrontal absent (L?; also in crocodylomorphs).
18) Atlantal intercentrum enlarged, completely surrounding odontoid ventrally and laterally and fitting into prominent recessed area below odontoid on axis.
19) Axial intercentrum, and then odontoid, fuses to axis at cessation of growth.
20) Modification of cervical centra and zygapophyses that combine to yield an S-shaped neck (compared to dinosaurs, rudimentary in both *Lagosuchus** and in Pterosauria ancestrally; although within pterosaurs the neck may be in some ways more birdlike than is the neck of *Archaeopteryx**).
21) Zygapophysial facets nearly vertically disposed in all but proximal part of tail (L?).
22) Interclavicle absent (L?).
23) Clavicle reduced and gracile (L?; enlarged in coelurosaurs).
24) Glenoid facet on scapulocoracoid faces posteroventrally (Pt?).
25) Coracoid small, with subcircular profile, and lying in nearly the same plane as the scapula (Pt?).
26) Forelimbs less than 55% of hindlimb length (Pt?), and hindlimb very long relative to length of trunk.
27) Apex of deltopectoral crest placed distally on humerus (Pt?).
28) Less than five phalanges in manal digit four and less than three phalanges in manal digit five (L?).
29) At least three vertebrae involved in sacrum (L?; also in Ornithosuchidae?).
30) Brevis shelf appears on ventral surface of postacetabular portion of ilium (Pt?).
31) Birdlike distal end of femur—prominent anterior and posterior intercondylar grooves, with the latter constricted by prominent external tibial condyle, and appearance of a discrete fibular groove and condyle—modifications in the knee joint played key roles in enabling a narrow-tracked, bipedal gait and erect stance (Stolpe 1932).
32) Tibia as long or longer than femur (reversed in all dinosaurs over a few meters in length, or larger in the case of theropods).
33) Fibula thin and strongly tapered distally and calcaneum reduced.
34) Astragalus transversely widened.
35) Astragalus and calcaneum with smooth, rollerlike articular surfaces abutting against depressed distal tarsals.
36) Metatarsals elongate and closely appressed.
37) Pes digitigrade.

38) Pes functionally tridactyl (Pt?).
39) Pedal digit five reduced, does not exceed length of metatarsal IV (Pt?), and composed of no more than two phalanges.
40) Parasagittal rows of osteoderms absent.

Dinosauria
(n. comb. =Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda—including birds)

Before proceeding with a diagnosis of Dinosauria, it will be necessary to briefly consider Herrerasauridae*, and the diagnoses of, and phylogenetic relationships within, Ornithischia and Sauropodomorpha.

Herrerasauridae* is represented by three very incompletely known taxa, *Staurikosaurus**, *Ischisaurus**, and *Herrerasaurus**, that are of uncertain relationships to one another. They nevertheless appear to be the sister-group(s) of all other dinosaurs (Gauthier 1984).

Diagnosis of Ornithischia

The diagnosis and contents of Ornithischia are unproblematic, which might be expected since the monophyly of this taxon has been accepted for nearly a century (Seeley 1887). The same cannot be said for phylogenetic relationships within Ornithischia. Using Saurischia as a sister-group, with herrerasaurs* and Pterosauria-*Lagosuchus** as successively more remote outgroups, the following characters are considered diagnostic of Ornithischia. The evidence discussed below is derived from Gauthier (1984) but modified in light of the studies of Sereno (1984, 1986) and Norman (1984). The only examples of relatively generalized ornithischians that were available for study were specimens of *Scutellosaurus** and a cast of *Heterodontosaurus*, and most of the characters listed below are derived from the literature (see review in Gauthier 1984).

Predentary bone; mandibular condyle set slightly to deeply below tooth rows; cheek teeth with distinct crown and root; crowns of cheek teeth low, bulbous basally, subtriangular in profile, and bear enlarged accessory denticles on margins; quadratojugal dorsal process reduced, not in contact with squamosal; ossified palpebral cartilage; antorbital fenestra reduced and much smaller than orbit; maxillary process of premaxilla enlarged and lengthened posteriorly to separate maxilla from nasal for half or more of their former sutural contact; quadrate elongate and massive; dentary participates in coronoid eminence; gastralia absent; ossified tendons present at least above sacral region; four to five or more sacral vertebrae and sexual dimorphism in sacral number (see Galton 1974, 1982); pubis completely reorganized, with short anterior process and long, rodlike posterior ramus paralleling ischium; ilium with enormously elongate iliac spine; symphysis restricted to distal end of ischium; winglike anterior trochanter; pendant fourth trochanter; fifth pedal digit reduced to metatarsal spur.

For the sake of discussion, I recognize the following basic taxa within Ornithischia:

1) *Lesothosaurus*
2) Thyreophora, a taxon including *Scutellosaurus**, *Scelidosaurus*, stegosaurs, and ankylosaurs
3) Following Sereno (1984, 1986), a taxon including *Heterodontosaurus* and Ornithopoda sensu Santa Luca (1980).
4) Following Sereno (1984), and Osmolska and Maryanska (pers. comm.), a taxon including pachycephalosaurs and ceratopsians (including psittacosaurs).

Taxon 1, *Lesothosaurus*, is very incompletely known. Its current placement in "Fabrosauridae" is uninformative; as conceived in Galton (1978) "fabrosaurs" are paraphyletic in that some taxa included within this group appear to be more closely related to the entity composed of ornithischian taxa 2–4 (hereinafter termed higher ornithischians), than they are to one another. *Lesothosaurus* is said to possess an obturator process on the ischium (Thulborn 1972), which is otherwise known only in Ornithopoda (Santa Luca 1980). However, other evidence indicates that *Lesothosaurus* is the sister-group of higher ornithischians (Gauthier 1984; Sereno 1984, 1986). That is to say, groups 2–4 share a mandibular fenestra that is very small or absent, a spout-shaped mandibular symphysis, slightly to deeply inset marginal tooth rows (i.e., structures analogous to "cheeks" are thought to have been present; Galton 1973*b*), a distal condyle of the quadrate that is wider than the mandibular condyle, an enlarged facial process of the maxilla that further reduces the size of the antorbital fossa and fenestra, a robust jugal, fused parietals, and an anterior pubic process that is at least moderately developed. Thus, in light of current knowledge it appears that an obturator process arose twice within Ornithischia.

*Scutellosaurus** is very poorly known, but it shares with the other members of taxon 2 raised osteoderms on the dorsum, an ilium that exceeds the length of the femur, and longer forelimbs and trunk compared to hindlimb length (Colbert, 1981). Accepting this placement requires that development of more deeply inset tooth rows took place twice within Ornithischia: once in the scelidosaur-stegosaur-ankylosaur group, and once in the remaining ornithischians. From evidence presented by Thulborn (1977), the so-called "juvenile scelidosaur" appears to bridge the gap between *Scutellosaurus** and the type-specimen of *Scelidosaurus* (Galton, pers. comm., considers the scelidosaur specimens conspecific). *Scelidosaurus*, stegosaurs, and ankylosaurs appear to be more closely related in that they share an enlarged palpebral covering the orbit dorsally; a hindlimb to trunk ratio of 0.85 or less, a tibia that is less than 80% of femur length; a metatarsal III that is less than 35% of femur length (ratios from Thulborn 1977); a relatively short, broad, and stoutly constructed manus and pes; and a stout postcranial skeleton. Within this assemblage, ankylosaurs and stegosaurs appear to be most closely related, although acceptance of this conclusion must await full preparation and description of *Scelidosaurus*. Stegosaurs and ankylosaurs share two additional osteoderms above the orbit; the absence of an antorbital fossa; a reduced or absent upper temporal fenestra; an inclined quadrate, a short neck and long torso; thick-walled limb bones; a more uniform width of the scapular blade and an enlarged acromial region of the scapulocoracoid; absence of a supra-acetabular buttress; femora with reduced fourth and anterior trochanters; a tibia that is less than 70–75% of femur length; a metatarsus that is only 25% of tibia length (ratios from Thulborn 1977), and very short, broad, and stout manus and pes bearing hooflike unguals. Most of these characters are associated with graviportal habits, and they appeared independently within ceratopsians and ornithopods (s.s.). One could thus argue that these characters could be collapsed into a single character related to large size and quadrupedal habits. Nevertheless, whether few or many, these data are accepted as indicating recency of common ancestry until there is evidence to the contrary.

Diagnoses of taxa 3 and 4 are left to Paul Sereno (1986). At this time I only wish to point out that both might be most closely related within Ornithischia, in that they share asymmetrically enameled tooth crowns, more deeply inset marginal tooth rows, at least five to six sacrals, and the absence of a supra-acetabular buttress. Moreover, these taxa are the only ornithischians in which a fully open acetabulum could be considered the ancestral condition. That is to say, although the acetabulum is completely perforate in some stegosaurs, it is only semiperforate in ankylosaurs, *Scelidosaurus*, *Scutellosaurus**, and *Lesothosaurus*. Thus, a semiperforate acetabulum with a supra-acetabular buttress is the ancestral condition for Ornithischia, and because this condition is also ancestral for Sauropodomorpha and Herrerasauridae*, a semiperforate acetabulum with a prominent supra-acetabular buttress also appears to be ancestral for Dinosauria.

The analysis of ornithischian phylogeny is not intended to be definitive. Nevertheless, the following conclusions appear secure.

1) Ornithischia is monophyletic.
2) *Lesothosaurus diagnosticus* appears to be the sister-taxon of all other ornithischians.
3) Although relationships among the major groups of ornithischians remain unclear, it is nonetheless evident that any character shared by *Hypsilophodon-Heterodontosaurus*, pachycephalosaurs-psittacosaurs-*Microceratops*, and *Scutellosaurus** and *Scelidosaurus* that is also present in *Lesothosaurus*, represents the ancestral condition for Ornithischia.

Diagnosis of Sauropodomorpha

Sauropodomorph monophyly is more problematic than that of Ornithischia (e.g., Charig et al. 1965). Nevertheless, using herrerasaurs*, and Pterosauria-*Lagosuchus** as successively more remote outgroups, the following characters are considered diagnostic of Sauropodomorpha, including such taxa as *Thecodontosaurus**, *Efraasia**, *Anchisaurus**, *Ammosaurus*, *Plateosaurus*, *Lufengosaurus*, segnosaurs, *Massospondylus*, *Riojasaurus*, *Vulcanodon*, *Barapasaurus*, and Sauropoda. The characters discussed below are derived primarily from the literature reviewed in Gauthier (1984), and were supplemented by examination of *Plateosaurus* specimens in Tubingen.

*Efraasia** and *Thecodontosaurus**, and to a lesser extent *Anchisaurus**, appear to be the most primitive sauropodomorphs. These taxa correspond to the "narrow-footed prosauropods" of Galton and Cluver (1976). Of course, the "broad-footed prosauropods" of Galton and Cluver (1976) are more closely related to sauropods, thus demonstrating the paraphyly of "Prosauropoda." *Efraasia** and *Thecodontosaurus** are too incompletely preserved to be very informative; nonetheless they share certain apomorphies diagnostic of Sauropodomorpha, first among them being the robust pollex and its enlarged claw noted above (also the hallux). In addition, the most recent common ancestor of *Efraasia**, *Thecodontosaurus**, *Anchisaurus**, and the more completely known sauropodomorphs, possessed lanceolate teeth with coarsely serrated crowns, a comparatively small skull suspended on a long neck composed of at least 10 cervicals, each of which is at least 25%

longer than are most of the trunk vertebrae, and a hindlimb that is subequal to or shorter than the trunk and in which the tibia is invariably shorter than the femur (reversed from ancestral condition in Ornithodira).

The remaining sauropodomorphs, including *Anchisaurus**, are further specialized compared to *Thecodontosaurus** in that they possess an even more robust first metacarpal and digit, wider-based neural spines on the anterior caudals, an arched dorsal margin of the ilium, and a completely open acetabulum.

Compared to *Anchisaurus**, and especially to *Thecodontosaurus**, the remaining sauropodomorphs are larger animals (this taxon will hereinafter be referred to as broad-footed sauropodomorphs). The broad-footed sauropodomorphs also share the following apomorphies: the mandibular condyle is set below the tooth row (also in *Efraasia**, which according to Galton [pers. comm.] actually represents a juvenile example of *Sellosaurus gracilis*); the internasal process of the premaxilla is compressed; the nares are very large owing to the previous character and emargination of the nasals; the teeth in the upper tooth row increase in height anteriorly and are especially long in the premaxilla (segnosaurs?); proximal caudal centra relatively compressed anteroposteriorly and with broad-based neural spines; robust forelimbs with a relatively shorter, broader, and stout manus, and to a lesser extent pes (i.e., broad-footed), with a greatly enlarged pollex; proximal carpals fail to ossify; acetabular fenestra is much larger than the size of the femoral head, and it was presumably filled with cartilage throughout life; and the initial development of a descending flange on the postero-distal end of the tibia (Cooper 1981*a*).

Although segnosaurs (*Erlikosaurus, Segnosaurus*) have been considered related to "theropods" (e.g., Barsbold 1983), or to represent relics of a transition between Ornithischia and "prosauropods" (Paul 1984*a, b*), segnosaur relationships appear to be with this subgroup of sauropodomorphs. Segnosaurs are remarkably specialized, with retroverted pubes, an edentulous and apparently beaked premaxilla like ornithischians, and very large ascending processes like coelurosaur and tyrannosaur theropods. In the context of all the evidence, however, these characters are here considered to have been acquired separately, and thus they are diagnostic of segnosaurs among sauropodomorphs.

Within the broad-footed sauropodomorphs, *Riojasaurus, Vulcanodon, Barapasaurus,* and Sauropoda appear to be most closely related. For example, the descriptions of *Vulcanodon* (Raath 1972) and *Barapasaurus* (Jain et al. 1975, 1979) reveal that these taxa share with Sauropoda the following characters that are absent in Sauropodomorpha ancestrally: spatulate teeth; strongly opisthocoelous cervical and anterior trunk vertebrae; cervical centra at least twice the length of midtrunk centra; deep, oval, "pleurocoelous excavations" below transverse processes; at least one more vertebrae added to sacrum (minimum of four sacrals); elongate neural spines confluent with one another in the sacrum; forelimb at least two-thirds of hindlimb length; ilium short anteroposteriorly and strongly arched in profile; brevis shelf reduced or absent; texture of articular surfaces of long bones indicates retention of thick pads of cartilage; distal tarsals fail to ossify; anterior trochanter reduced to a rugosity or absent; fourth trochanter reduced and displaced distally to near middle of femur; femur robust, thick-walled, wider laterally than anteroposteriorly, and with straight shaft; tibia to femur ratio less than 0.63; tibia compressed side to side and cnemial crest reduced; enlarged descending flange on posterior face of distal end of tibia; metatarsal III less than 37% of tibia length; metatarsals subequal in length and arranged in a shallow arch, with a broad, very short and stoutly constructed pes with a hooflike ungual on pedal digit three; fourth and fifth pedal digits without clawlike unguals.

As the following list of synapomorphies attests, sauropod monophyly is a highly corroborated hypothesis.

Relatively short postorbital region of skull that is strongly inclined posteroventrally, thus making the skull appear flexed about the braincase in lateral view; frontals and parietals wider than long; very long nasal process of premaxillae (absent in many diplodocids); nasals deeply excavated to form posterior margins of retracted external nares; postorbital reduced to a thin, elongate bar extending nearly to ventral surface of orbit; posterior and postorbital processes of jugal reduced; dorsal process of quadratojugal reduced in that it fails to reach squamosal, but anterior process enlarged and nearly reaching maxilla; lacrimal thin and elongate posterodorsally, forming most of anterodorsal margin of orbit; narrow process of maxilla extends over antorbital fenestra nearly to anterodorsal margin of orbit; lower temporal fenestra inclined anteroventrally to extend well below orbit; palate abbreviate, with broad choana; pterygoid flanges blunt and well anterior to braincase; epipterygoid absent; tooth rows entirely antorbital and anterior teeth procumbent; mandibular fenestra absent; at least two vertebrae added to cervical series (minimum of 12 cervicals); cervical ribs fused to centra in fully adult specimens; vertebrae with highly cancellous to cavernously pleurocoelous centra surrounded by dense lamellar bone; tall neural spines in posterior part of trunk, over sacrum, and in anterior caudal vertebrae; at least one vertebra incorporated into sacrum (=five or six sacrals); relatively broad sacrum with enlarged sacral transverse processes that are level with top of deeply arched ilium; massive proximal caudals; greatly enlarged acromial region of scapulocoracoid, resulting in pronounced demarcation between scapular blade and base of scapula; metacarpals stout and arranged in a hemispherical colonnade below the forearm (Note: The fourth and fifth metacarpals and digits are set on the palmar surface of the hand in Saurischia ancestrally, thus initiating the cupped metapodial unit that is taken to extreme in sauropods; compare *Massospondylus* in Cooper 1981*a*, fig. 37, with *Brachiosaurus* in Janensch 1922); manus elephantine, only digit one retains the ancestral phalangeal formula and a large, clawlike ungual, with the others being reduced to single phalanges supporting hooflike unguals (phalangeal formula 2-1-1-1-1, as opposed to 2-3-4-3-2, the ancestral condition for Dinosauria); pubis ventrally directed and more massively developed than ischium; puboischiadic junction robust; forelimbs at least three-fourths of hindlimb length (may be less in diplodocids); limbs massive, vertically disposed, long bones nearly solid (sauropods appear to be one of the few dinosaur groups with a truly vertical, parasagittal, limb posture); tibia with narrow descending flange; pes stout, very short and broad, phalanges of outer digits short, with digit three losing three phalanges (phalangeal formula 2-3-4-2-1 as opposed to 2-3-4-5-1); gastralia absent.

Sauropoda may be divided into two principal groups, here referred to informally as camarasaurs and titanosaurs. Camarasaurs share a strongly arched internarial bar of the premaxilla, a snout that is sharply demarcated from the rest of the skull, a relatively elongate ischium that extends well posterior to the level of the ilium while twisting to become more horizontally disposed distally, and a relatively very deep puboischiadic contact.

Euhelopus (Wiman 1929) may be the sister-taxon of the titanosaurs; both taxa share a quadrate that slants up and back from the mandibular condyle, neural spines that are slightly to deeply bifurcate (convergent in *Camarasaurus*), and the incorporation of three or more trunk vertebrae into the cervical series.

For the sake of discussion, titanosaurs will be divided into two informal taxa: the antarctosaurs for such taxa as *Antarctosaurus, Alamosaurus, Laplatasaurus,* and *Titanosaurus,* that share a caudal series in which the first centrum is biconvex and subsequent caudals are procoelous; and diplodocids for *Apatosaurus, Barosaurus, Cetiosauriscus, Dicraeosaurus, Diplodocus, Mamenchisaurus,* and *Nemegtosaurus,* that share diagnostically modified haemal arches with fore-and-aft projections, midsacral neural spines that are deeply cleft, and ischia that are expanded distally.

The phylogenetic analysis of Berman and McIntosh (1978) established titanosaur monophyly in that antarctosaurs and diplodocids possess the following synapomorphies: snout long, broad, and depressed; body of premaxilla and supraantorbital process of maxilla extend dorsally to level of orbit, internasal processes of premaxilla and nasals reduced or absent, and nasals very short, thus external nares are confluent on midline and situated high on skull; lacrimal very reduced; dorsal process of quadratojugal very reduced and anterior process broadly in contact with maxilla at anteroventral margin of orbit; very long basipterygoid processes of basisphenoid; elongate, pencil-like teeth confined to anteriormost part of jaws; neural spines in posterior cervical and anterior trunk vertebrae deeply cleft and V-shaped in anterior view (convergent in *Camarasaurus*); sacral neural spines very tall; very long tail forming distal whip-lash consisting of a long series of cylindrical caudals; relatively short forelimbs that are approximately two-thirds of hindlimb length; and metatarsal IV exceeds the length of metatarsal III.

The preceding discussion of sauropodomorph phylogeny establishes the following points.

1) Broad-footed sauropodomorphs are monophyletic.
2) Evidence currently available indicates that *Anchisaurus** could be the sister-group of the broad-footed group, and that the group composed of both these taxa would form an unresolved trichotomy with *Efraasia** and *Thecodontosaurus**. Thus, Sauropodomorpha appears to be monophyletic.
3) Sauropoda is monophyletic.
4) Such as they are known, *Riojasaurus,* and especially *Vulcanodon* and *Barapasaurus,* appear more closely related to Sauropoda than are other broad-footed sauropodomorphs.
5) Thus, any character that is present in broad-footed sauropodomorphs, that is also present in *Anchisaurus**, *Efraasia**, and *Thecodontosaurus**, is considered to have been present in Sauropodomorpha ancestrally

Diagnosis of Dinosauria

Given that (1) Ornithischia, Sauropodomorpha, and Theropoda are each monophyletic; and (2) accepting that any character shared by *Lesothosaurus* and higher ornithischians, *Efraasia**-*Thecodontosaurus** and broad-footed sauropodomorphs, and *Procompsognathus**-*Liliensternus** and ceratosaurs represents the ancestral conditions for Ornithischia, Sauropodomorpha, and Theropoda respectively; and (3) accepting that herrerasaurs* and *Scleromochlus**-*Lagosuchus** rep-

resent successively more remote outgroups, Dinosauria can be diagnosed by the following synapomorphies.

41) Vomers elongate, reaching posteriorly at least to level of antorbital fenestra (also in aetosaurs?).
42) Scapula at least three times longer than width at base, and entire scapulocoracoid further inclined posterodorsally (also in pterosaurs aside from *Scleromochlus**).
43) Increased asymmetry of hand, with small outer two digits having fewer phalanges (ancestral phalangeal formula for: Archosauria =2-3-4-5-3; Ornithodira =2-3-4-4-?; and Dinosauria =2-3-4-3-2).
44) Semiperforate acetabulum and prominent supra-acetabular buttress (T. Rowe, pers. comm., notes that the inner wall of the acetabulum is thin in semi-erect archosaurs. Thus, it is not surprising to see the independent appearance of this character in fully erect ornithosuchids, and in some fully erect crocodylomorphs and rauisuchians. The acetabulum becomes fully perforate at least three times within Dinosauria, once in ornithischians, once in sauropodomorphs, and once in theropods. The degree to which the acetabulum is open also varies with absolute size; with the exception of ankylosaurs, the larger the dinosaur the more open the acetabulum).
45) Birdlike femur and antitrochanter: medial rotation about long axis of element of that portion of femur proximal to fourth trochanter (=inturned head of femur); proportional elongation of femoral shaft distal to anterior trochanter; dorsal arc of entire femoral shaft; fore-and-aft compression of femoral head in proximal view; and femoral head more distinctly set off from shaft of femur. Also, modifications of the distal end of the femur noted above are more prominent in dinosaurs. These modifications are also accompanied by reorientation of the antitrochanter, which faces mostly dorsally in archosaurs ancestrally, but faces mainly ventrally in dinosaurs (T. Rowe, pers. comm.). The proximal end of the femur in pterosaurs like *Dimorphodon* (Padian 1983) is in some ways more birdlike than is that of *Lagosuchus** (Gauthier 1984).
46) Anterior trochanter enlarged.
47) Dinosaur tibia: cnemial crest prominent and with weakly crescentic profile in dorsal view (size and shape of cnemial crest varies with size of animal and style of locomotion). Distal end of tibia broadened mediolaterally, thus element appears twisted nearly 90° with respect to proximal end. And with prominent fossa on anterolateral face of distal end of tibia for reception of ascending process
48) Birdlike ankle: proximal tarsals fit caplike onto tibia and fibula; crurotarsal joint and calcanear tubercle absent; ascending process of astragalus present (i.e., intermedium moves dorsally)—thus, motion within the ankle confined mainly to a simple, hingelike joint between the rollerlike proximal and the compressed, distal tarsals. (Like the femur, the ankle joint in pterosaurs appears to be more dinosaurlike than that of *Lagosuchus**; these apomorphic similarities suggest a monophyletic pterosaur-dinosaur group [Ornithotarsi, n. txn.], as argued in Gauthier 1984).
49) Pedal digit five shorter than metatarsal I; the foot is tridactyl in the typical dinosaurian condition.

One of the key elements in the dinosaur controversy is the problem presented by Sauropodomorpha. Charig et al. (1965) and Charig (1976*a, b*) argued that the erect, quadrupedal pose of Sauropoda was an ancestral condition for dinosaurs, and that theropods and ornithischians acquired their bipedal habits independently (Charig accepts that the quadrupedal pose of some ornithischians is secondary). As Cooper (1981*a*) pointed out, some taxa are easily relegated to particular locomotor categories. For example, sauropods are probably obligate quadrupeds, and theropods obligate bipeds, but a number of taxa are not so readily placed in either category (e.g., the sauropodomorph *Massospondylus*). Whether we view this problem from the perspective of observed morphology or from that of inferred functions, we are still left with Charig's problem: are sauropodomorphs ancestral or apomorphic in these regards? That is to say, the ancestral dinosaur could have been a cursorial biped (or considering the role of the tail, a triped), and sauropodomorphs could subsequently have reacquired quadrupedal habits. Alternatively, the common ancestor of dinosaurs could have been a pachypodal quadruped, with ornithischians and theropods subsequently becoming bipedal cursors independently of one another as Charig suggested. Either hypothesis requires the same number of evolutionary events, and if one is unwilling to make assumptions about the probability of reversals versus convergences, these data alone do not afford a basis for choice. This question can, however, be evaluated by reference to additional outgroups (Maddison et al. 1984). Given that taxa such as *Staurikosaurus**, *Scleromochlus**, and *Lagosuchus** represent outgroups, it appears likely that the ancestral dinosaur was a small, erect-postured, cursorial biped.

The same kind of analysis can be used to address the question of the ancestral dinosaur morphology. Using the dinosaur foot as an example, it is interesting to note that the foot is gracile, elongate, and functionally tridactyl in *Lagosuchus**, herrerasaurs*, theropods, and in ornithischians ancestrally. Although the fourth toe (and finger) and fifth toe are unusually long in pterosaurs, the proportions and lengths of the middle three toes are like those of birds and unlike those of either pseudosuchians or ornithosuchians ancestrally (Padian 1983; Gauthier 1984). Consequently, the simplest explanation for the shorter, stouter, and tetradactylous foot of Sauropodomorpha is that these conditions represent apomorphic reversals.

In fact, sauropodomorphs are unique among archosaurs in the size and shape of the first finger and toe. The hand in particular is strikingly modified even in early sauropodomorphs. Galton (1971) and Baird (1980) discussed the relations between the articular surfaces of the metacarpal and first phalanx in manal digit I (the pollex) in early sauropodomorphs (="prosauropods"). They noted that adjacent articulations within the pollex were modified so that upon maximum extension the enormous ungual phalanx was directed medially and thus was nearly horizontally oriented. Upon flexion, however, the claw was brought into the same line of action taken by the other digits.

Baird (1980) described a fossil trackway of an *Ammosaurus*-like sauropodomorph walking quadrupedally. In a most elegant test of a functional hypothesis based on an extinct organism, Baird used the morphology of the trackway to show that the manus functioned as predicted. Indeed, the manus was held in an essentially digitigrade pose, with the digits fully extended so that the enlarged claw was laid flat upon its side against the substrate. Perhaps the unusual modifications of the pollex reflect divergent functional demands placed on the hand in the larger sauropodomorphs (five meters and above). Stout forelimbs and powerful, grasping hands may have supported the role of the head and neck as cropping organs while in a bipedal (or tripodal) feeding pose (Bakker 1971), by providing secure purchase on the trunks of trees. This and other possible roles of the grasping hand and enlarged first claw would have to be balanced against the role of the hand as a weight-bearing structure during quadrupedal locomotion. Perhaps these factors combined to yield the unusually modified pollex of sauropodomorphs.

With regard to the problem of the history of the tridactyl foot, it is most interesting to note that in sauropodomorphs the modifications of the first finger (pollex) apply as well, albeit less dramatically, to the first toe (hallux). The modifications shared by the pollex and hallux cannot be accounted for by invoking functional similarity. Rather, as Davis (1964) argued in the case of the panda's thumb, simultaneous modification of the hallux and pollex suggests that it was simpler to alter the developmental program of both limbs than to change that of the hand alone. Of course, whatever accessory roles the hand may have played early in sauropodomorph history, these functions were overwhelmed by the demands of weight-bearing in Sauropoda. Thus, the tetradactylous impressions of hind feet attributed to some sauropodomorphs do not represent an ancestral condition; on the contrary the modified hallux is as diagnostic of sauropodomorphs as is the uniquely modified pollex.

In conclusion, the ancestral dinosaur was essentially birdlike. It had a mobile, S-shaped neck, a short trunk, and long hindlimbs with modified joints that enabled a narrow-tracked gait. Its short forelimbs, together with other modifications in the hands and girdles, indicate that the forelimbs were suited less to performing roles in support and locomotion than they were to grasping and manipulating food. As argued by Bakker and Galton (1974), a variety of structural modifications indicate that the primary responsibility for support and locomotion had shifted to the hindlimbs and girdles in the ancestral dinosaur. That the ancestral dinosaur was a bipedal cursor is especially evident in the morphology of its tail, in the elongate and narrow distal portions of its hindlimbs, and in its functionally tridactyl and digitigrade pes. By the standard of typical Mesozoic dinosaurs, the ancestral dinosaur was quite small. Indeed, using other ornithodirans as outgroups, one might infer that it was certainly under two meters and perhaps under one meter in total length. Although small, the ancestral dinosaur would have had a broad visual horizon because of the birdlike pose of its neck and hindlimbs. Considering these modifications as a whole suggests that the ancestral dinosaur was small, cursorial, erect and normally bipedal. Its divergently specialized fore- and hindlimbs indicate that the ancestral dinosaur was capable of more than the mere facultative bipedality it inherited from its saurian ancestors. On the other hand, trackways indicate that forelimbs could still play a role in support and locomotion at low speed, so the ancestral dinosaur was not so locked into this mode of progression as are its obligately bipedal living relatives.

The main points of the foregoing discussion of archosaur phylogeny may be summarized as follows (and see Fig. 7).

1) Archosauria is composed of the sister-groups Pseudosuchia and Ornithosuchia.
2) Parasuchia is the sister-group of all other pseudosuchians, and *Euparkeria** appears to be the sister-group of all other ornithosuchians.
3) Within Ornithosuchia, Ornithosuchidae is the sister-group of Ornithodira (n. txn.).

4) Ornithodira (n. txn.) is erected to encompass an unresolved trichotomy composed of *Lagosuchus**, Pterosauria, and Dinosauria.
5) Dinosauria is a monophyletic taxon composed of the metataxon Herrerasauridae*, and the monophyletic sister-groups Ornithischia and Saurischia.

Appendix B

Taxon/Character Matrix for Saurischia Data Set

The following matrix consists of the eighteen taxa and eighty-four characters that were subjected to PAUP. Character states coded 0 denote ancestral conditions and character states coded 1 denote apomorphic conditions. Characters coded 9 indicate either that the region of the skeleton was not preserved, or that it was too poorly preserved to be certain of state assignment, or that the region in question was too transformed to allow unambiguous state assignment (i.e., the ectopterygoid has yet to be identified in birds, so the condition of the element cannot be coded). The reader is referred to discussions of individual characters in the text for caveats, variation, and rationale for state assignments. The characters are listed in vertical columns by taxon, beginning with character 1 on the left and ending with character 84 on the right. To facilitate reference with numbered character discussions in text, the characters are divided into groups of five.

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Addendum

1) Continuing research on early dinosaur phylogeny revealed an additional synapomorphy for Saurischia, the lateral overlap of the quadratojugal onto the posterior process of the jugal. Archosauromorpha is diagnosible in part by a long posterior process of the jugal that extends nearly to the end of the lower temporal fenestra to overlap laterally the anterior process of the quadratojugal (Gauthier 1984; e.g., Fig. 1A, B). The ornithodiran (see Fig. 7) quadrate no longer displays the anterodorsal to posteroventral slope characteristic of early archosaurs. Consequently, neither the ventral portion of the lower temporal fenestra nor the posterior process of the jugal are as long as in archosaurs ancestrally. Nevertheless, the jugal still has a prominent lateral overlap onto the quadratojugal in dinosaurs ancestrally (Fig. 1C, D). Just the opposite relations between these bones obtain in saurischians, however, because the quadratojugal wraps around the ventral margin of the jugal, extending up the lateral face of that element to gain broad exposure on the lateral surface of the skull (Fig. 1E–K). This apomorphy is also shared by *Hesperornis* (Gingerich 1976), so the saurischian condition appears ancestral for birds as well.

2) As noted in Part V, character 78, above, there is no unequivocal evidence in the literature for the orientation of the pubis in troodontids. Because troodontids and dromaeosaurs appeared to be sister-groups (Ostrom 1969*a, b*; Colbert and Russell 1969), I tentatively accepted that, as in dromaeosaurs and birds, the pubis was reversed in Troodontidae. This assumption now appears mistaken. During a recent visit to the American Museum of Natural History to study *Saurornithoides mongoliensis*, I discovered that the pubis was probably not reversed in Troodontidae.

Osborn mentioned, but did not figure or describe, a bone-bearing concretion lying near to that containing the type skull "which may belong to the same individual" (1924*b*:3). This concretion, now completely prepared, contains portions of a postcranial skeleton including a partial, associated pelvis; the pubis is incomplete, but it clearly retains the ancestral, anteroventral orientation. This fact, together with new information on troodontid anatomy (Currie in press *a, b*), casts further doubt on the monophyly of Deinonychosauria. At this point, the only theropods in which a reversed pubis has been identified with certainty are *Deinonychus*, *Velociraptor*, and Avialae.

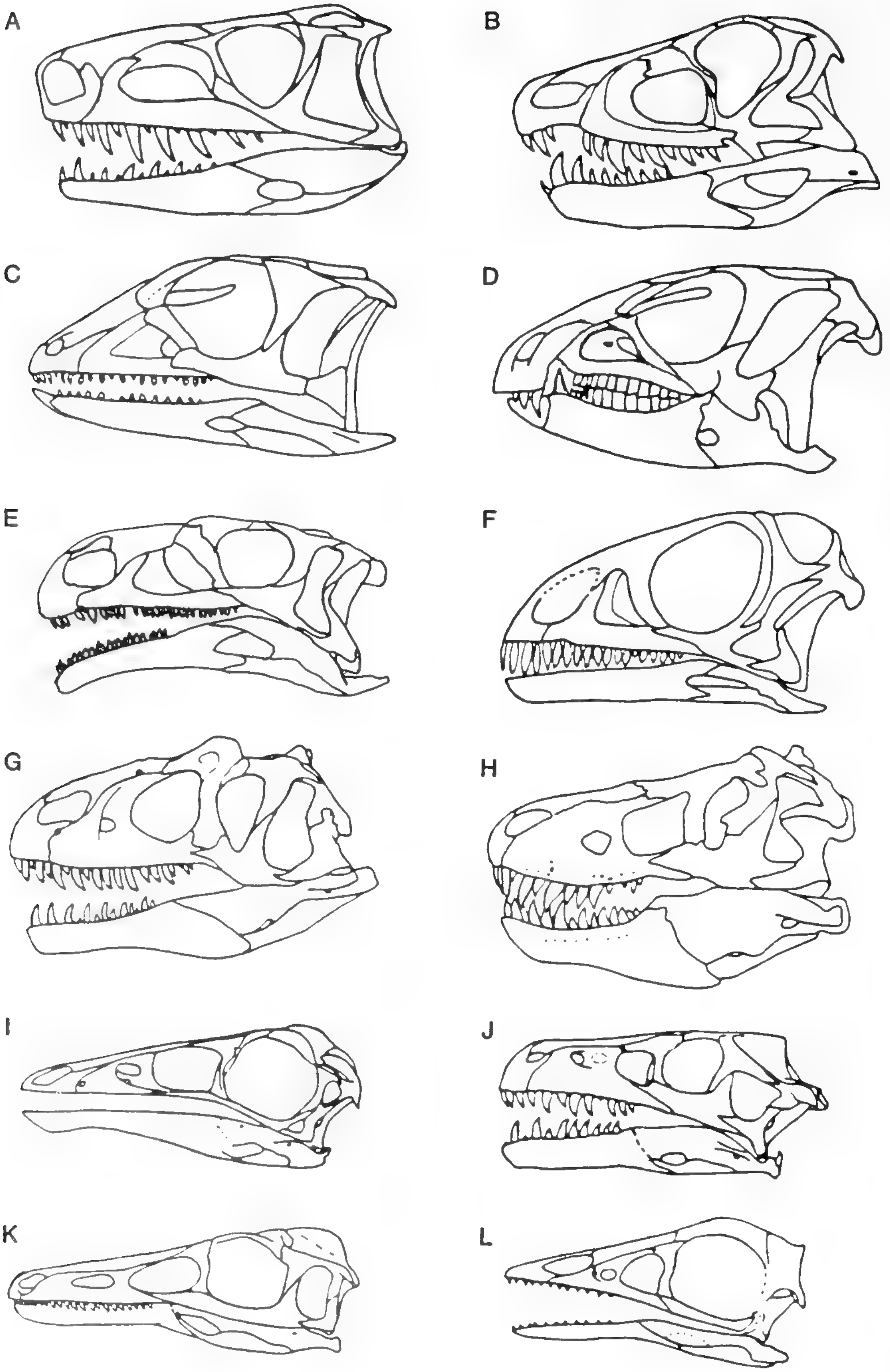

FIGURE 1. Skulls in lateral view: A) *Euparkeria capensis**; B) *Ornithosuchus longidens* (Ornithosuchidae); C) *Lesothosaurus diagnosticus* (Ornithischia); D) *Heterodontosaurus tucki* (Ornithischia); E) *Plateosaurus engelhardti* (Sauropodomorpha); F) *Massospondylus carinatus* (Sauropodomorpha); G) *Allosaurus fragilis* (Carnosauria); H) *Tyrannosaurus rex* (Carnosauria); I) *Dromiceiomimus brevitertius* (Ornithomimidae); J) *Dromaeosaurus albertensis* (Dromaeosauridae); K) *Saurornithoides mongoliensis* (Troodontidae); L) *Archaeopteryx lithographica** (Avialae). Drawing A after Ewer (1965); B after Walker (1964); C after Galton (1978); D after Chang (1979); E after Galton (1984); F after Cooper (1981*a*); G after Madsen (1976); H after Romer (1956); I after Russell (1972); J after Colbert and Russell (1969); K after Russell (1969); L after Ostrom (1976*a*)

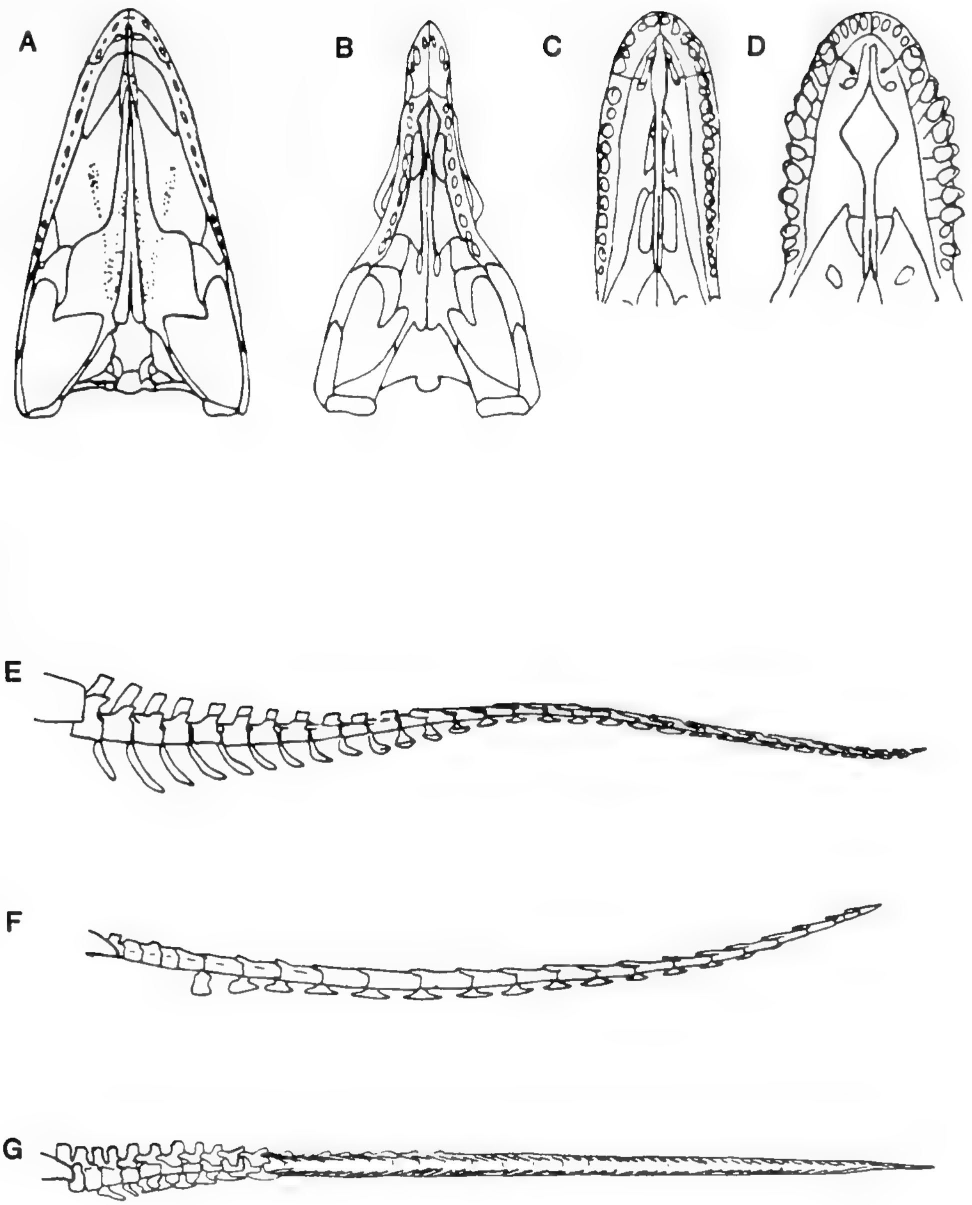

FIGURE 2. Skulls in ventral view: A) *Euparkeria capensis**; B) *Ornithosuchus longidens* (Ornithosuchidae); C) *Allosaurus fragilis* (Carnosauria); D) *Tyrannosaurus rex* (Carnosauria). Caudal series in lateral view: E) *Dromiceiomimus brevitertius* (Ornithomimidae); F) *Archaeopteryx lithographica** (Avialae); G) *Deinonychus antirrhopus* (Dromaeosauridae). Drawing A after Krebs (1976); B after Walker (1964); C after Madsen (1976); D after Romer (1956); E after Russell (1972), F after Ostrom (1976*a*); G after Ostrom (1976*b*).

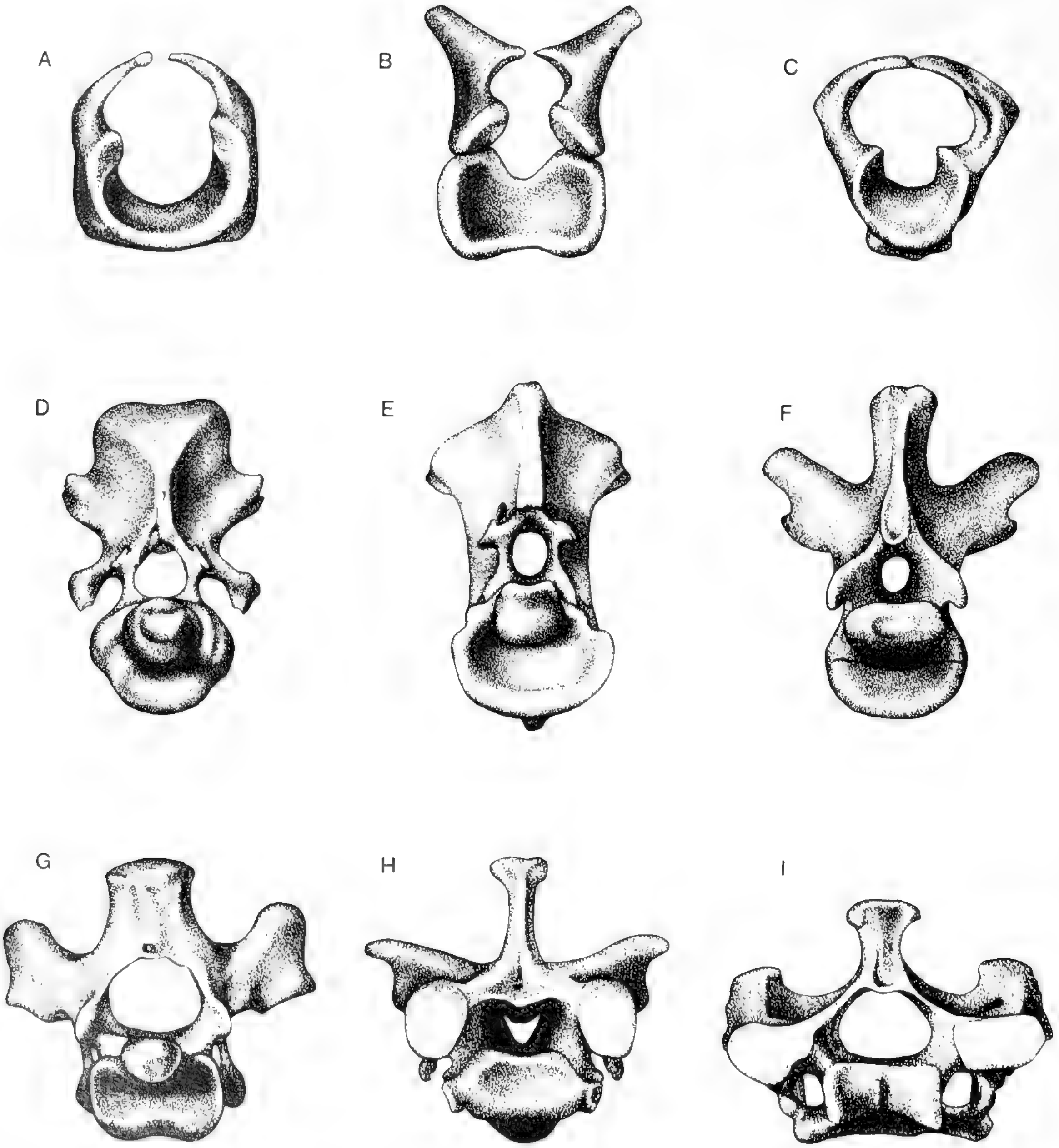

FIGURE 3. Anterior views of atlas (A–C), axis (D–G), cervicals 3–4 (H, I): A) *Stegosaurus stenops* (Ornithischia); B, E) *Ceratosaurus nasicornis* (Ceratosauria); C, G, I) *Apteryx australis* (Aves); D) *Camarasaurus grandis* (Sauropodomorpha); F, H) *Deinonychus antirrhopus* (Dromaeosauridae). Drawing A, D after Ostrom and McIntosh (1966); B, E after Gilmore (1920); F, H after Ostrom (1969*b*).

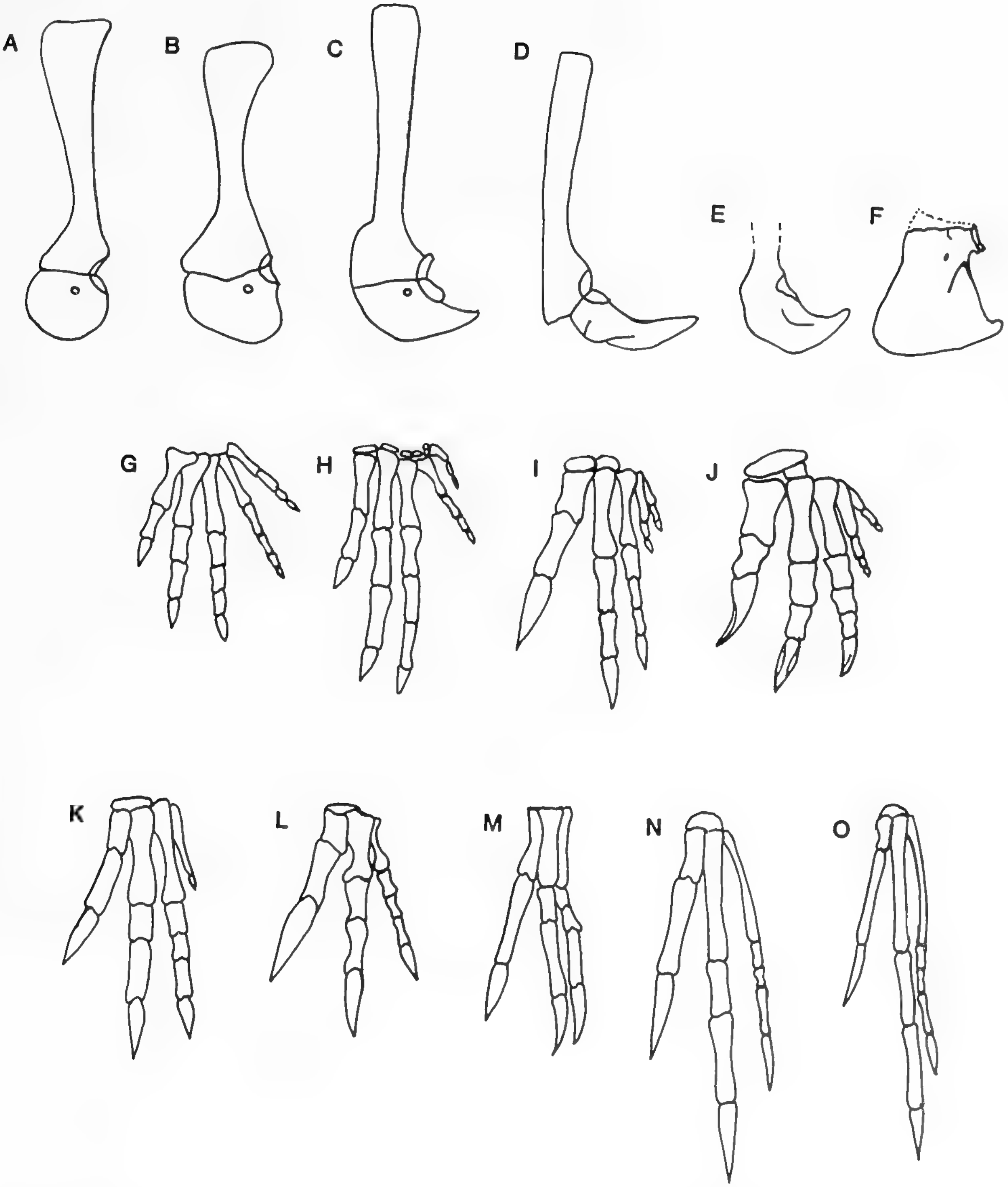

FIGURE 4. Scapulocoracoids in lateral view: A) *Heterodontosaurus tucki* (Ornithischia); B) *Massospondylus carinatus* (Sauropodomorpha); C) *Gallimimus bullatus* (Ornithomimidae); D) *Archaeopteryx lithographica** (Avialae); E, F) *Deinonychus antirrhopus* (Dromaeosauridae). Left manus in dorsal view: G) *Crocodylus* sp. (Crocodylomorpha); H) *Heterodontosaurus tucki* (Ornithischia); I) based on *Thecodontosaurus antiquus** and *Efraasia diagnostica** (Sauropodomorpha); J) *Massospondylus carinatus* (Sauropodomorpha); K) *Syntarsus rhodesiensis* (Ceratosauria); L) *Allosaurus fragilis* (Carnosauria); M) *Struthiomimus altus* (Ornithomimidae); N) *Deinonychus antirrhopus* (Dromaeosauridae); O) *Archaeopteryx lithographica** (Avialae). Drawing A, H after Santa Luca (1980); B, J after Cooper (1981*a*); C after Osmolska et al. (1972); D, E after Ostrom (1976*a*); F after Ostrom (1974*b*); G after Romer (1956); I partly after Bakker and Galton (1974) and Huene (1932); K after Raath (1969); L after Madsen (1976); M after Osborn (1917); N after Ostrom (1976*a*); O partly after Ostrom (1976*a*).

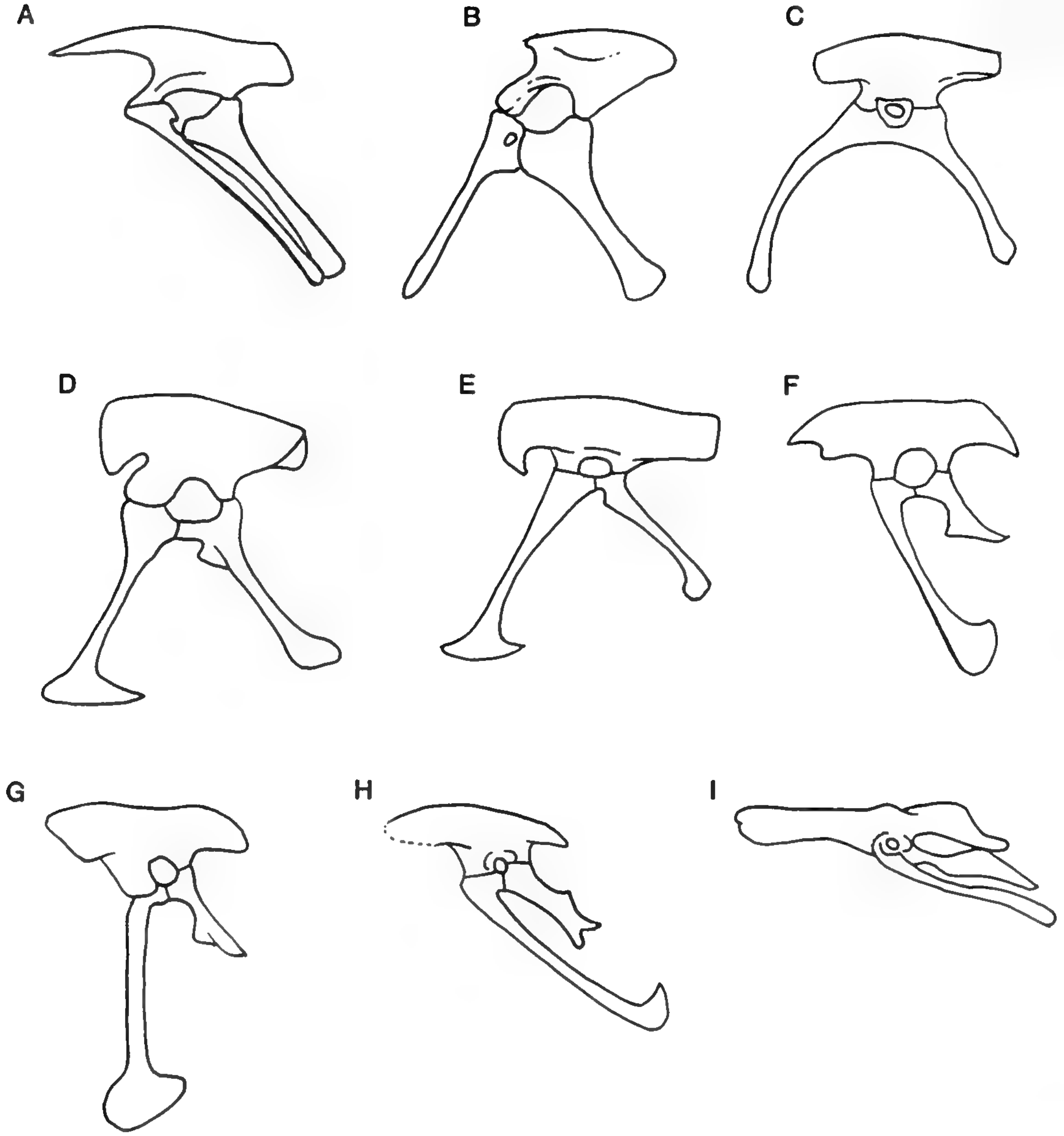

FIGURE 5. Pelvic girdle in lateral view: A) *Scelidosaurus* (Ornithischia); B) *Massospondylus carinatus* (Sauropodomorpha); C) *Coelophysis bauri* (Ceratosauria); D) *Allosaurus fragilis* (Carnosauria); E) *Gallimimus bullatus* (Ornithomimidae); F) *Adasaurus mongoliensis* (Dromaeosauridae); G) *Deinonychus antirrhopus* (Dromaeosauridae); H) *Archaeopteryx lithographica** (Avialae); I) *Apatornis celer* (Ornithurae). Drawing A after Charig (1976*b*); B after Cooper (1981*a*); C after Raath (1969); D after Madsen (1976); E after Osmolska et al. (1972); F after Barsbold (1983); G after Ostrom (1976*b*); H after Ostrom (1976*a*); I after Marsh (1880).

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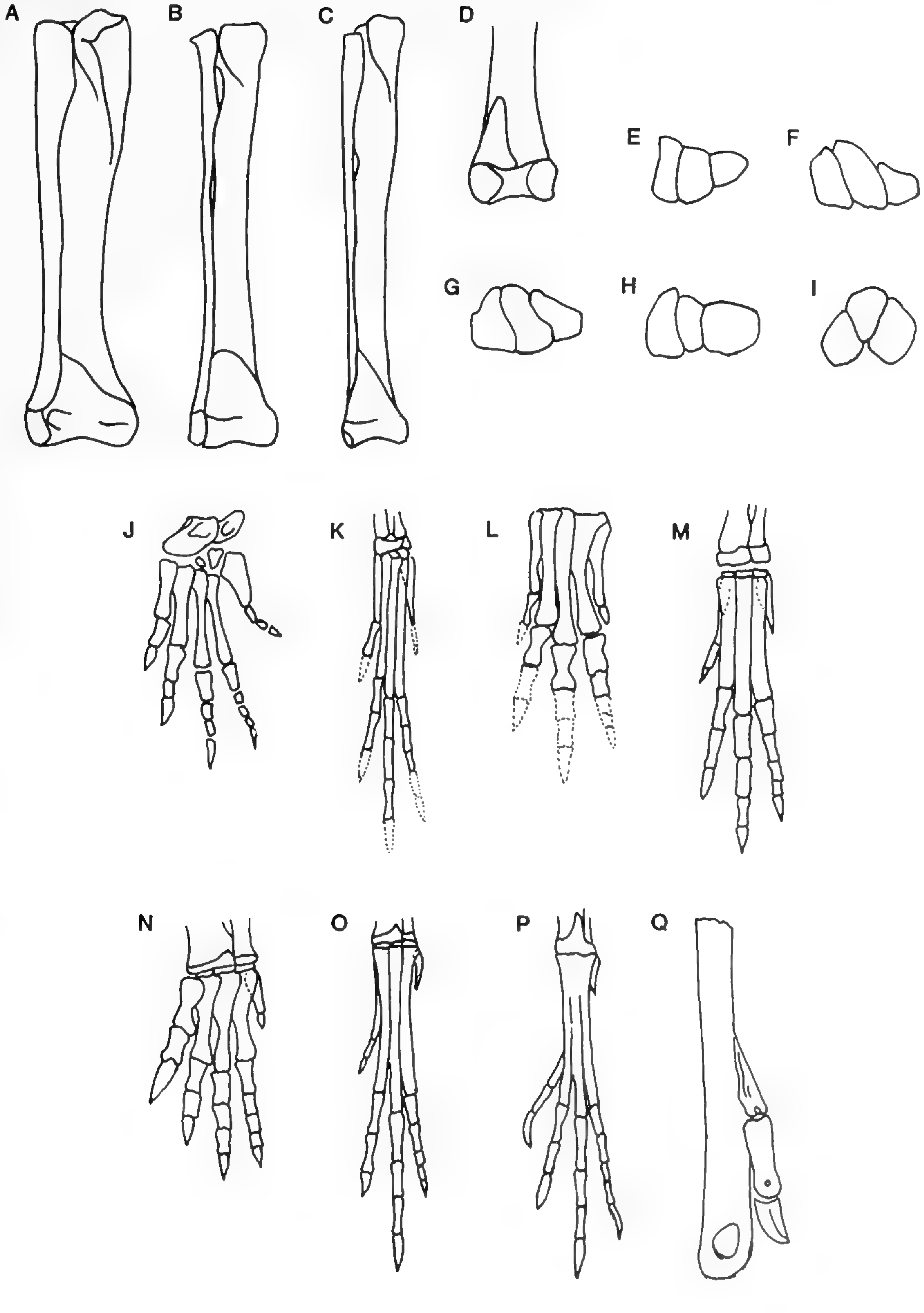
FIGURE 6. Tibia, fibula, and proximal tarsals in anterior view: A) *Allosaurus fragilis* (Carnosauria); B) *Deinonychus antirrhopus* (Dromaeosauridae); C) *Gallimimus bullatus* (Ornithomimidae). Distal end of tibiotarsus in anterior view: D) *Baptornis advenus* (Ornithurae). Metatarsals II, III, and IV in proximal view: E) *Hypsilophodon foxi** (Ornithischia); F) *Dilophosaurus wetherilli* (Ceratosauria); G) *Allosaurus fragilis* (Carnosauria); H) *Deinonychus antirrhopus* (Dromaeosauridae); I) *Apteryx australis* (Aves). Left pes in dorsal view: J) *Euparkeria capensis**; K) *Lagosuchus talampayensis**; L) *Herrerasaurus ischigualastensis** (Herrerasauridae*); M) *Lesothosaurus diagnosticus* (Ornithischia); N) *Anchisaurus polyzelus** (Sauropodomorpha); O) based on *Procompsognathus triassicus** (Theropoda *incertae sedis*), and *Segisaurus halli** and *Dilophosaurus wetherilli* (Ceratosauria); P) *Archaeopteryx lithographica** (Avialae). Medial view of articulation between digit I and metatarsal II: Q) *Compsognathus longipes* (Coelurosauria). Drawing A, G after Madsen (1976); B after Ostrom (1976*b*); C after Osmolska et al. (1972); D after Martin et al. (1980); E after Galton (1974); F after Welles (1984); G after Gilmore (1920); H after Ostrom (1969*b*); J after Cruickshank (1979); K after Bonaparte (1975*a*); L after Reig (1963); M after Bakker and Galton (1974); N after Marsh (1896); P after Ostrom (1976*a*); Q after Tarsitano and Hecht (1980).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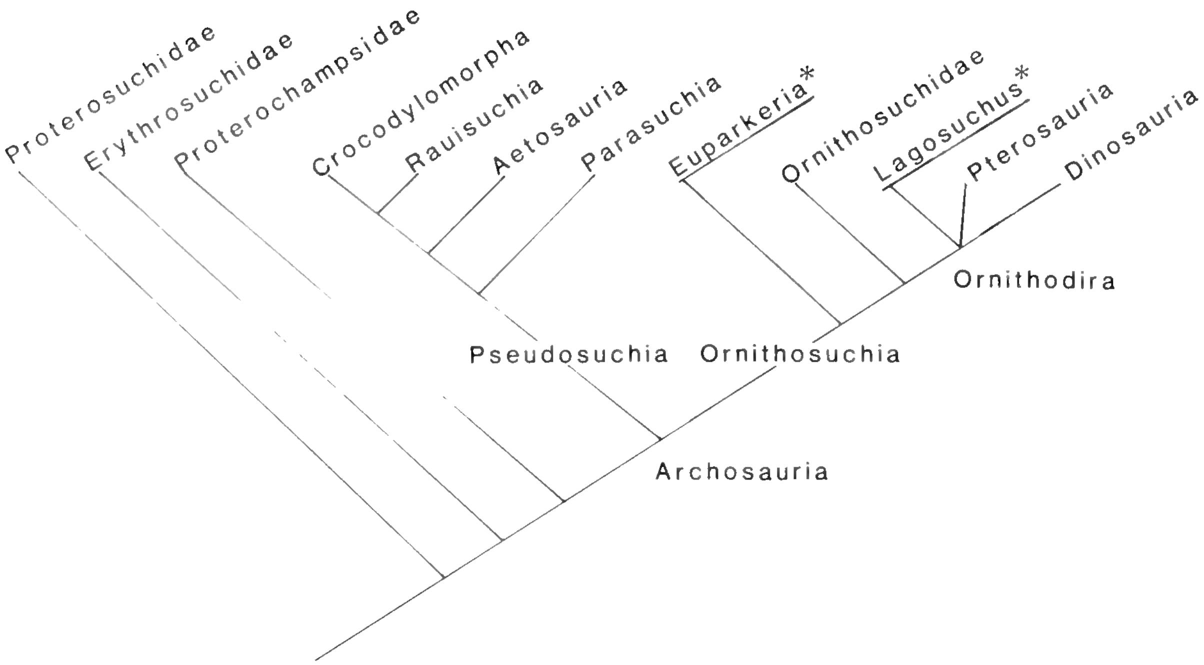

FIGURE 7. Cladogram depicting phylogenetic relationships among Archosauria.

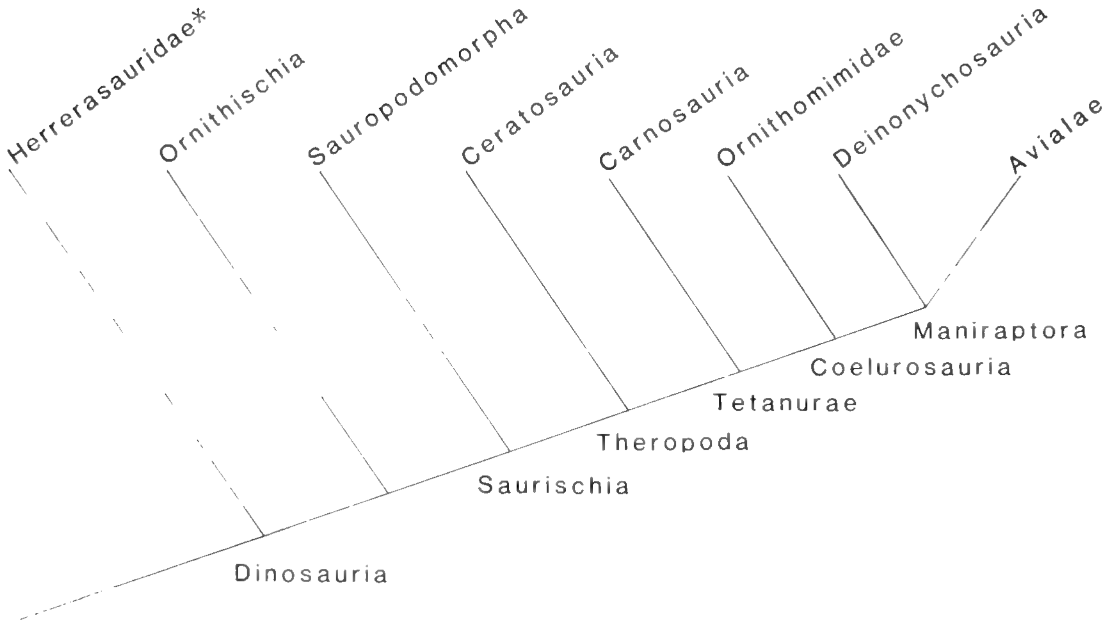

FIGURE 8. Cladogram depicting phylogenetic relationships among comparatively well known theropods and other dinosaurs.

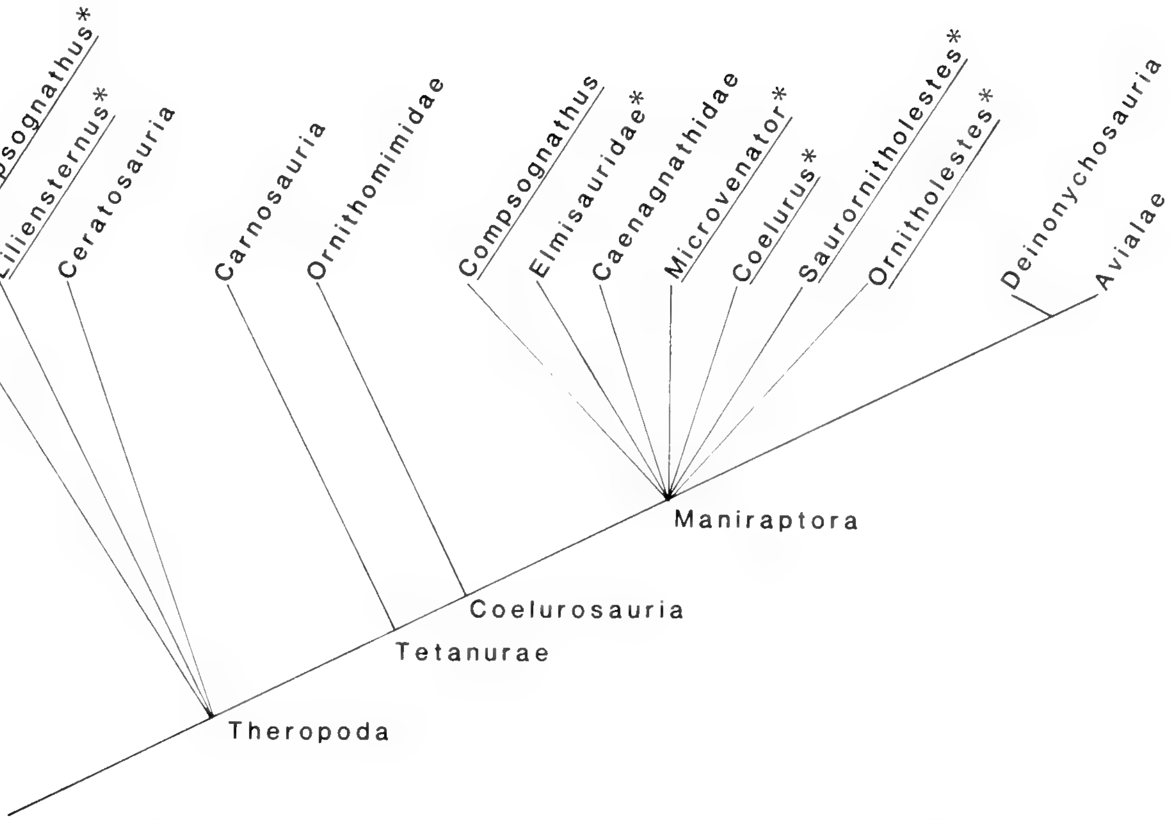

FIGURE 9. Cladogram depicting phylogenetic relationships among all theropods considered in this analysis.

The Arboreal Origin of Avian Flight

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Introduction

After the discovery of the first three recognized specimens of *Archaeopteryx lithographica*—the original feather, the London specimen, and the Berlin specimen—ornithologists and other vertebrate zoologists initially wanted to show that this fossil was a true intermediate form, "a missing link," between reptiles and birds, and that it thus provided support for the then new Darwinian theory of evolution. A second concern was the analysis of *Archaeopteryx's* precise reptilian ancestry. General consensus was reached that *Archaeopteryx,* and hence birds, descended from some member of the great archosaurian radiation, but there was little agreement on a more definite ancestral group. Almost immediately explanations were offered for the evolution of avian flight. Williston (1879) proposed the cursorial theory of avian flight, and Marsh (1880) proposed the arboreal theory (see Ostrom 1974, Stephan 1974, and Feduccia 1980, for excellent summaries of diverse ideas on the evolutionary origin of avian flight). These conflicting theories, with modifications, have been actively debated to the present day. Much of the earliest discussion was vague because the understanding of the physics of flight, and hence of the necessary intermediate evolutionary stages leading to flight, was inadequate. The pioneering studies of the Lilienthal brothers in Germany were underway during the 1880s (see O. Lilienthal 1889). When Otto Lilienthal died in 1896 in a glider crash, these studies were continued alone by Gustav Lilienthal (see G. Lilienthal 1925). In France, Etienne Jules Marey (1890) undertook the first important physiological investigations of avian flight. Some general reviews of avian flight including historical comments can be found in Storer (1948), Herzog (1968), and Rüppell (1977).

This early period of discussions ended when the authoritative and now classic *The Origin of Birds* was published by the Danish worker Gerhard Heilmann (1926). Heilmann argued strongly against the cursorial theory for the origin of avian flight especially as presented by Nopcsa (1907, 1923) and advocated the arboreal theory in which an initially terrestrial runner became an arboreal climber, then a leaper between branches and from trees to the ground, a glider, and finally an active flier (Heilmann 1926:197–201). Although Heilmann provided inadequate support for a number of his conclusions by today's standards, his analysis was extremely advanced for the mid-1920s. His basic arguments and conclusions were accepted by most workers for the next 50 years, and many of his ideas are still valid today.

Partly because Heilmann's study was so complete, relatively little was published on *Archaeopteryx* for the next 30 years. The modern period of *Archaeopteryx* studies was ushered in with the publication of de Beer's (1954*a*) monograph on the London specimen and his discussion (1954*b*) of the pertinence of *Archaeopteryx* to evolutionary ideas. With the discovery or recognition of three additional specimens between 1956 and 1973, including the excellent Eichstätt specimen, studies on *Archaeopteryx* and the evolution of birds and avian flight flourished (see Ostrom 1975, 1976*a* for excellent reviews; and the proceedings of the recent Eichstätt symposium, Hecht et al. 1985). In the 30 years since the appearance of de Beer's monograph in 1954, more papers have been published describing the morphology of *Archaeopteryx,* discussing the relationships of *Archaeopteryx,* and analyzing the evolutionary origins of birds and of avian flight than during the previous 90 years. The thriving *Archaeopteryx* industry that developed shows no signs of decline. The result has been much new information on the morphology of this primitive bird and numerous ideas on many aspects of avian evolution.

One consequence of this renewed activity was a modern restatement of the arboreal theory for the evolution of avian flight (Bock 1965, 1969, 1983) and a revival of the cursorial theory by Ostrom (1974, 1976*b,* 1979). More recently the cursorial theory was also championed by Caple et al. (1983, 1984) and by Padian (1982*a, b,* 1983). The modern cursorial theory as advocated by Ostrom differs markedly from that advanced by Nopcsa, and those proposed by Caple et al. and by Padian differ again from that of Ostrom. The differences between the arboreal and the cursorial theories for the origin of avian flight are striking, with a major distinction being the direction of movement of the initial flight (be it gliding or active flapping) with respect to the downward pull of gravity. In arboreal theories, movement of the protobird is downward from a higher point in trees toward the ground in the direction of gravitational pull. The animal obtains most or all of the force required for movement through the air from the pull of gravity. In cursorial theories, movement of the protobird is from the ground upward into the air to a higher point and opposite to the direction of the pull of gravity. Thus, the animal's primitive flight apparatus must provide force against gravity plus additional force to accelerate the animal upward. Recently some workers (e.g., Hecht and Tarsitano 1982; Peters 1984, 1985) postulated that protobirds may have glided downward from a height such as a cliff, rather than from trees, toward the ground. This argument seems to have been taken up by some proponents of the cursorial theory, but is not yet in print.

This paper will examine the evidence supporting the arboreal theory for the origin of avian flight and contrast the arboreal and cursorial theories. I specify an arboreal theory, not just the argument that avian flight evolved from the heights downward. Protobirds are postulated to be in trees not only for the origin of flight but to account for the evolution of several features (e.g., homoiothermy and feathers) associated with flight and some features present in *Archaeopteryx* (e.g., detailed structure of manal claws). I shall discuss those avian features involved directly or indirectly with the evolution of avian flight, but these will be examined in conjunction with the evolution of all essential avian features to at least the stage of primitive, active flapping flight. This analysis of the evolution of these features will stress consideration of their possible functions and adaptive significances;

hence, the discussion must include comments on possible environments and selective demands arising from them. Most importantly, the evolution of these individual features will be scrutinized in terms of how they contribute to the operation of the entire organism. That is, the analysis will be holistic on the level of the organism as strongly advocated by Gutmann (e.g., 1977, 1981) and on the level of the organism-environmental interaction as stressed by von Wahlert (1965, 1968, 1978; von Wahlert and von Wahlert 1977). This analysis will be based on the concept of historical-narrative explanations as advocated by Bock and Caplan (In press) and on the synthetic explanation of macroevolutionary change (Bock 1979).

As much as possible, the theoretical ideas will be related to the available fossil evidence. But I must stress at the start that this evidence is far scantier than indicated by many workers. What is available is the morphology of the skeleton, the flight feathers, and the horny covering of the claws of *Archaeopteryx*. These features are reasonably well known as a result of the many descriptive studies of the five known skeletal fossils of this organism. But *Archaeopteryx* is only one stage in the evolution of modern birds from reptiles. Furthermore, we know nothing about *Archaeopteryx*'s soft anatomy, including the muscular system, ligaments, and cartilaginous structures; its physiology; behavior; ecology; and general way of life. The guesses that must be made in any explanation of the evolution of avian flight overwhelm whatever factual evidence can be obtained from detailed study of the available *Archaeopteryx* specimens.

Although general agreement exists that *Archaeopteryx*, and hence birds, descended from an ancestor within the great archosaurian radiation, little agreement exists on a more precise ancestral group. Heilmann (1926:183–191) concluded that birds evolved from the pseudosuchians (Thecodontia), a conclusion that was generally accepted for the next 50 years. In his thorough review of the ancestry of birds, Ostrom (1976*a*) surveyed the several divergent ideas of ancestral groups. A major problem is that the thecodontian suborder Pseudosuchia is not clearly delimited from the several archosaurian orders that presumably evolved from them. Ostrom (1976*a*) argued against an ornithischian ancestry of birds and compared the evidence for the theropod ancestry (which he favored), the thecodont (pseudosuchian) ancestry, and the crocodylomorph ancestry (Walker 1972) of birds. Ostrom concluded that *Archaeopteryx* evolved from a small coelurosaurian (theropod) dinosaur, a conclusion accepted by many other workers. Tarsitano and Hecht (1980) demurred and advocated the earlier thecodont theory of Heilmann. Walker (1977), Whetstone and Martin (1979), and Martin et al. (1980) supported the crocodylomorph ancestry of birds. Evidence exists supporting each of these theories (see also the Eichstätt symposium, Hecht et al. 1985), but the available empirical evidence is not reasonably convincing for or against any one theory. Part of the problem stems from the fact that the three proposed ancestral groups are closely related and are not sharply distinguishable from one another morphologically. Part of the problem stems from difficulties in describing certain critical features in *Archaeopteryx* and making the needed comparative analyses. And part of the problem stems from an inadequate knowledge of the pseudosuchians. I do not believe that the question of the precise reptilian ancestry within the Archosauria is resolvable at this time. Moreover, resolution of this problem is not critical to the question of the evolutionary origin of avian flight. To my knowledge, the three proposed ancestral groups of *Archaeopteryx*—the pseudosuchians (Thecodontia), early Crocodylomorpha, and the coelurosaurian dinosaurs (Theropoda)—do not differ significantly in the features pertinent to discussions of the evolution of avian flight. Hence, for the purposes of this paper, it does not matter which of the three proposed groups within the Archosauria is the ancestor of birds. The ancestral conditions of the characters to be discussed for the evolution of avian flight are basically the same in all three groups as far as is known.

Apart from the problem of the evolutionary origin of birds, a second consideration is whether *Archaeopteryx* is or is not in the direct line of evolution to modern birds and hence whether or not features possessed by *Archaeopteryx* are primitive for birds. Recently several workers (e.g., Martin 1985) have implied that *Archaeopteryx* is on a sideline in the evolution of birds and hence that its characteristics are not necessarily primitive for birds. In view of the lack of agreement on the possible archosaurian ancestor of birds and the lack of any other avian fossils until the late Cretaceous, except for isolated bones for which the phylogenetic affinity within birds cannot be established (e.g., *Ambiortus dementjevi:* Ambiortiformes, Kurochkin 1982, 1985), no support exists for the hypothesis that *Archaeopteryx* is not in the direct lineage of birds. The morphological features of *Archaeopteryx* must and will be used in my analysis of the evolution of avian flight.

The Arboreal Theory

The arboreal theory for the origin of avian flight that I advocate is consistent with, but not identical to, the major aspects of the theory proposed by Heilmann (1926). The two key features of the arboreal theory are that protobirds lived in trees and that flight originated by locomotion through the air from the trees downward toward the ground. The starting point was a terrestrial ancestral reptile, presumably with quadrupedal locomotion. At some point, protobirds went up into trees and spent part of their life in trees and part of their life on the ground. Protobirds could climb up the tree trunks, scramble about on branches, and leap from one branch to another nearby branch as do present-day squirrels. Protobirds could also climb down the tree trunks or otherwise reach the ground. Possibly they leaped from a low branch, or from the trunk, to the ground. With evolutionary change and specialization, protobirds probably first parachuted (unspecialized glide with a steep angle of descent) to the ground and subsequently became more and more specialized gliders. Gliding led to active flapping flight. During the early stages of flight (e.g., gliding and primitive flapping flight) most of the energy for flight came from the downward pull of gravity. Only in the more specialized stages of flapping flight did much of the energy for flight come from flight muscles. During the entire period of the evolution of flight, protobirds spent part of their life on the ground, probably for feeding.

I consider *Archaeopteryx* to have been a specialized glider but not an active flapping flier. It would have had to climb up into trees, but could have glided down to the ground. And it would have spent part of its life on the ground.

I argue against cursorial theories for the origin of avian flight. These theories postulate that protobirds were ground-dwellers even though the authors may have stated that *Archaeopteryx* might have also spent some time in trees. Flight evolved from

the ground up into the air against the pull of gravity. All of the published cursorial theories (Ostrom 1974; Padian 1982*a, b;* Caple et al. 1983, 1984) state clearly that flight was from the ground up into the air. All of these theories imply, or state clearly, that protobirds were not tree-dwellers until after active flight had evolved. These theories postulate that active flight started with flapping of the wings for some purpose such as extending the distance of the leap, and that gliding was not a stage prior to active flapping flight. I also argue against theories postulating that active flight originated by the protobird jumping off steep slopes or cliffs and moving downward through the air with the pull of gravity (Hecht and Tarsitano 1982), but for different reasons (e.g., evolution of homoiothermy, reversed hallux).

Thus the basic differences between the arboreal and cursorial theories are as follows: (a) flight that evolved as locomotion through the air from a higher position, in trees, downward toward the ground, versus flight that evolved as locomotion through the air from the ground upward into the air; and (b) protobirds that lived on the ground until after the evolution of active flight versus protobirds that lived in trees before the evolution of active flight.

Important differences between these theories are the postulated habitat and the way of life of protobirds plus *Archaeopteryx.* The arboreal theory assumes that protobirds were partly ground-dwelling, presumably for feeding, and that some avian features evolved in response to selective agents arising from the terrestrial part of the protobirds' environment. Further, it also assumes that protobirds were partly tree-dwelling, presumably for hiding, sleeping, and nesting, and that other avian features evolved in response to selective agents arising from the arboreal past of the protobirds' environment.

Trees could have been used originally as a place of safety from most predators. Possibly trees originally served as a hiding and resting place and then as a sleeping roost at night. Subsequently trees could have been used as a reproductive site—the place where a nest was built and the eggs were laid and incubated. Evolutionists usually underestimate or completely overlook the importance of many aspects in the life of animals. Hiding and sleeping sites are most significant, and reproductive sites are essential in the life of animals. Protobirds probably did not use trees as a feeding site until they reached a relatively advanced stage in their evolution to modern birds, that is, not until after they were active flapping fliers.

Unfortunately many workers have argued for a more restricted habitat for protobirds and *Archaeopteryx.* Most workers who support a cursorial theory for the origin of avian flight have assumed that protobirds could have lived either on the ground or in the trees, but not both (see Ostrom 1974:33–34, 1976*b:* 18–19, 1979:51–53; his statements are equivocal in that he admits that *Archaeopteryx* could have lived in trees, but his entire analysis is presented for a strictly terrestrial way of life for protobirds, including *Archaeopteryx,* until after flapping flight was achieved). Ostrom and other cursorial proponents argue that some features seen in *Archaeopteryx,* such as bipedalism, could only have evolved for a terrestrial way of life and that other features, such as feathers on the forearms and tail and the avian forearm linkage system, would have been in conflict with arboreal life. Thus trees are ruled out as a possible part of the environment for protobirds, and flight would have had to evolve from the ground upward into the air. The basic premise of the argument that protobirds could have lived either on the ground or in trees, but not both, is unjustified; hence the rest of the cursorial argument does not follow.

A number of present-day birds live in a complex habitat exactly analogous to that postulated herein for protobirds and *Archaeopteryx.* The Cracidae, a group of neotropical gallinaceous birds, are an excellent example. They spend much of their time feeding on the ground, but fly up to trees as a place of safety, for roosting, for sleeping at night, and for nesting (Delacour and Amadon 1973). Many water birds have a similar division of life. Much of their life is spent on the open water of oceans, lakes, or rivers, but these birds nest on land either on islands, on cliffs, or in trees. Marsh birds such as herons and storks spend their days feeding in marshes, but most species roost and breed in trees. Other species frequently breed on a site far removed (up to 50 km) from their feeding areas with the breeding sites carefully chosen as places of safety far removed from predators. An excellent example is the South American Grey Gull (*Larus modestus*), which lives on the Pacific Ocean coast but nests inland in the hot, bone-dry deserts along the west coast of South America. Breeding colonies are located about 30–50 km inland from the ocean in an area where no predators exist (Howell et al. 1974). In all of these cases, each species has some features that are adaptations to selective agents arising from the feeding habitat and other features that are adaptations to selective agents arising from the nesting habitat.

Thus, no basis exists for assuming that the habitat of an animal must be a restricted one. Certainly no justification exists for assuming that protobirds and *Archaeopteryx* must have lived exclusively in trees or exclusively on the ground. And there is no reason to assume that just because some features (e.g., the structure of the hindlimbs) in *Archaeopteryx* appear to have been adapted to selective agents arising from dwelling on the ground, *Archaeopteryx* could not also have lived in trees. If it could be demonstrated that protobirds and *Archaeopteryx* spent part of their lives in trees, it would be far easier, and much more realistic, to postulate an evolutionary origin of flight from the trees down to the ground rather than from the ground up into the air.

Avian Flight Features

In this section I consider only features associated with the evolution of avian flight, not all features of *Archaeopteryx* or all features involved in the origin of birds. Many of these latter features, regardless of how interesting they may be, do not bear directly on the explanation of the evolution of avian flight, on the flying ability of *Archaeopteryx,* or on the merits of rival theories for the origins of avian flight.

I. Homoiothermy and Feathers

These two characters are usually not discussed in any detail because homoiothermy is not preserved in fossils and because feathers are already fully evolved in *Archaeopteryx.* Thus, other than knowing that feathers evolved very early in the reptilian-avian transition, no fossil evidence exists for the evolution of avian feathers. (A peculiar fossil has been described by Rautian [1978] as an avian feather, *Praeornis sharovi.* This fossil has been cited by some workers [e.g., Peters 1984, 1985] as an early

stage in the evolution of the typical avian feather. I examined this fossil, through the courtesy of Dr. E. N. Kurochkin, while I was in Moscow in 1979 and 1981. I can confirm the original description of Rautian, but not the interpretation. The central shaft and the secondary projections appear to be too coarse to be a feather the size of this fossil. Moreover, if it were a feather, it would have come from a large animal, one at the upper limit of the range of body sizes of known flying birds. I believe this fossil to be more similar morphologically to the pinnate leaf of a cycad than to an avian feather. The original description by Rautian did not explain why he considered this fossil to be avian and not a plant.)

Most workers agree that homoiothermy was a prerequisite for the evolution of avian flight, but I am unaware of a really convincing argument supporting this idea. The most reasonable argument is not based on the high metabolic requirement associated with flight (for which the flight muscles must be as warm as possible) but on the need for immediate high muscular output when an animal begins to fly, be it gliding or active flapping. When a modern bird launches itself into flight, the muscles must generate considerable force immediately and must maintain this high level of force development. No time exists for a warm-up or for the muscles to develop force slowly as the muscles of a terrestrial tetrapod could when it starts to move. Once a modern bird has been actively flying for some minutes, the muscles have warmed up and the problem may be how to lose heat rather than how to maintain the elevated temperature of the flight muscles. The same requirements would exist for flight in protobirds. I tentatively accept the conclusion that homoiothermy, with an elevated body temperature close to the critical temperature for the central nervous system, would have been a precondition for the evolution of flight in birds.

Homoiothermy in a small vertebrate, the size of *Archaeopteryx,* requires an insulating cover on the body, which prevents excessive loss of heat from the animal to the external environment. Hence homoiothermy in protobirds implies an insulating body covering, such as feathers. However, feathers and even full, body plumage in protobirds does not necessarily imply homoiothermy, because feathers could have evolved originally under the control of selective agents not associated with preventing excessive heat loss in a homoiothermic animal (Regal 1975).

Parkes (1966) agreed with Heilmann's (1926:200) conclusion that feathers evolved for aerodynamic purposes from elongated scales along the trailing edge of the forelimb, the lateral edges of the tail, and possibly along other edges of the body. The elongated scales would have provided greater surface to the body—a larger airfoil—which would be advantageous in parachuting and gliding.

Regal (1975) argued that the early evolution of feathers was associated with regulation of heat flow between the animal and its external environment, but that the explanation was much more complex than simple insulation to prevent heat loss in protobirds. Regal pointed out that many reptiles have body temperatures elevated above that of the ambient temperature; they obtain the extra heat from external sources, mainly solar radiation, and have a high degree of control of their body temperature. Reptiles, like birds and mammals, have an upper lethal temperature at which the central nervous system is irreversibly damaged. As Regal stressed, a major problem facing these reptiles is overheating, and hence irreversible damage to the central nervous system, while in the sun during the hot part of the day. Facultatively homoiothermic reptiles have evolved a number of morphological, physiological, and behavioral features to prevent excessive heat flow into the body when the animal is overexposed to solar radiation. (By facultative homoiothermy I mean the ability to maintain a reasonably constant, elevated body temperature using an external source of heat [solar radiation]. In the absence of an external heat source, body temperature drops, and the animal becomes sluggish.)

Regal postulated that feather evolution started in reptilian ancestors of birds by elongation of the scales to provide sun shades for the body and hence to reduce heat flow into the body of these facultative homoiotherms. As the scales became longer and longer during evolution, they became relatively rigid. Regal postulated that the formation of transverse slits from the lateral edges almost to the midline would have increased the flexibility of the scale and decreased the danger of damage. The result was a structure with lateral plates (protobarbs) attached to a central shaft. Narrowing of the lateral plates and their secondary subdivision would have led to the evolution of barbs and barbules. The spinules present on the surface of scales of many reptiles may have evolved into the hamuli of the barbules or possibly into the barbules themselves. All of these changes would have been associated with the evolution of longer, more flexible, and more efficient heat shields.

Once pennaceous feathers evolved as a heat shield in facultative homoiothermic protobirds, these structures reached a preadapted stage and could serve as an insulating covering to prevent heat flow out of the body of an obligatory homoiotherm. And when the feathers were well developed, with a central shaft and vane formed by interlocking barbs, the feathers reached a second preadapted stage—structures that could enlarge the airfoil of the wings and the tail. Elongation of the original body feathers along the posterior edge of the wings and along the lateral edges of the tail as flight feathers would be similar to the evolution of feathers from scales as postulated by Heilmann and Parkes.

I accept the narrative for the evolution of avian feathers advanced by Regal (1975) for the reasons that he presents. Therefore I conclude that fully developed avian feathers and homoiothermy most probably evolved in protobirds prior to the appearance of the most rudimentary level of flight.

The evolution of obligatory homoiothermy in birds and in mammals is a major evolutionary step, one that has received far too little attention from vertebrate zoologists and paleontologists discussing the evolution of these groups (Regal and Gans 1980; see also Thomas and Olson 1980). Obligatory homoiothermy probably evolved from facultative homoiothermy. In obligatory homoiotherms, a constant, elevated body temperature is maintained using internal heat sources, for example, burning metabolic food supplies. Heat, and hence energy, is constantly lost to the external environment. An upper lethal temperature exists as in facultative homoiotherms, and a variety of physiological and behavioral mechanisms regulate body temperature. Body temperature does not drop in obligatory homoiotherms with a decrease in ambient temperature (except under special conditions such as hibernation), the animals remain ac-

tive. Obligatory homoiotherms require large amounts of food to maintain their constant body temperature; the need to obtain and assimilate food on a constant basis necessitated the evolution of major modifications in the digestive system of these animals (Karasov and Diamond 1985). They must be more active feeders and must utilize a high energy habitat compared to that of facultative homoiotherms. This difference can be easily seen by comparing the energy requirements of reptiles to those of mammals with the same body mass. Evolutionary changes in obligatory homoiotherms associated with obtaining and processing larger amounts of foods are major ones and would include the ability to travel rapidly to feeding grounds and modifications of the digestive system, in addition to the obvious changes in the feeding apparatus.

In addition to shifts in food requirements, the evolution of obligatory homoiothermy involves a number of major structural changes. A complete separation of the heart into two parallel pumps and hence a total separation of the pulmonary and somatic circulatory systems must occur. Morphologically this is an easy step, but it has major consequences for other parts of the body. The whole pulmonary circulatory system must be modified because of increased blood flow to the lungs, and presumably the lungs changed because of the greater blood flow and pressure. A large part of the somatic circulatory system may also have changed because of shifts in blood flow and pressure.

If the changes associated with the evolution of homoiothermy in birds are so expensive, which selective agents might have controlled this evolution, and which factors in the external environment of protobirds might have given rise to these selective agents? These factors must have been significant ecological demands having major influences on the fitness of individual organisms in populations of protobirds. These evolutionary modifications associated with the origin of obligatory homoiothermy were as decisive as those connected with the subsequent evolution of avian flight, and possibly more so.

Birds are basically diurnal animals and seem to have been so in all stages in their evolution from their reptilian ancestors. Avian groups such as the Strigiformes (owls) and Caprimulgiformes (nightjars) are clearly derived; they evolved their nocturnal adaptations subsequent to the evolution of modern birds. Presumably the reptilian ancestors of birds were terrestrial; at least no one has suggested otherwise. Considering the general habits of terrestrial, diurnal reptiles, the energetic cost of homoiothermy, and the large number of associated morphological and physiological changes, I find it difficult to conceive of any set of environmental conditions and hence of any set of selective agents associated with ground-dwelling in a basically daytime creature that would result in the evolution of obligatory homoiothermy. None of the suggestions available in the literature, for example, cool conditions in the shadows of dense forests or the cool conditions of cliff faces, are convincing.

The evolution of obligatory homoiothermy in mammals appears to have been for completely different reasons than birds. Mammals are basically nocturnal, terrestrial animals and appear to have been so ever since the earliest stages in their evolution from mammal-like reptiles. Hence homoiothermy in mammals probably evolved because of selective demands arising from nocturnal life. Quite possibly these selective demands were connected with the need to maintain high body temperatures and the ability for quick action in small protomammals while resting, sleeping, or moving very slowly (e.g., slow stalking of food, waiting motionlessly in ambush for prey) during the cool nighttime hours.

I postulate that obligatory homoiothermy evolved in protobirds as a result of selective agents associated with environmental demands and habits of these animals in trees. Several significant aspects of arboreal life differ sharply from those of terrestrial life for homoiothermic animals, both facultative and obligatory. Trees are considerably cooler than the ground as there is more wind, more shade when the tree is leafed out, and less reflected heat from the surface of the ground. The decrease in ambient temperature from the ground up is quite rapid, especially when the sun is shining directly on the ground. For example, Howell et al. (1974) have shown that Grey Gulls standing on rocks 15–20 cm above the surface of the desert are considerably cooler than gulls standing on the desert floor or sitting on nests and are therefore able to maintain a body temperature below the upper lethal limit with greater ease. Thus, if protobirds were partly or mainly arboreal, they would have had greater problems maintaining a constant elevated body temperature while in trees than while on the ground. This would have been true for both facultative and obligatory homoiotherms.

Trees could have been used in a number of ways by early protobirds. They could have served as an escape refuge, as a hiding place, or as a resting site both during the day and at night. I doubt that trees were originally used as a feeding area for protobirds. These uses of trees would have involved the animal being inactive or moving very slowly, and hence generating little body heat. An additional use of trees by protobirds, one that probably evolved subsequent to the use of trees as an escape, hiding or resting site, is as a nesting site. Nesting in trees may have been most important for the evolution of obligatory homoiothermy in birds. It could have been highly advantageous for protobirds to place the nest and eggs in trees rather than placing them on the ground or burying them in the ground. In trees, the nest and eggs would have been more protected as they would have been removed from the reach of predators, assuming that most of the small tetrapod egg predators of that time lived on the ground. Nests in trees are difficult to see and hard to locate by smell until the predator is right on the nest. These difficulties are clearly demonstrated by asking ornithologists how many bird nests they have found even when actively searching for them. Today, ground-nesting birds generally suffer much more from predation on the eggs and young, especially from terrestrial predators, than do tree-nesting species.

Arboreal nesting sites are generally cooler than terrestrial sites, and the chances of getting extra heat from solar radiation is much less because of greater shading. Thus success of arboreal nesting in protobirds would have been correlated closely with the ability of the adult to supply heat to the eggs, especially during the night. An animal incubating eggs on the nest would have been inactive and its metabolic rate would have been low, close to or at basal metabolism. An arboreal nest with adult incubation would have led to a longer nesting life for the young and hence to the evolution of parental care. All of these factors would have increased the fitness of individuals and would have been strongly favored by selective agents.

I would like to stress several points relating to the evolution

of homoiothermy. First, researchers should consider aspects of life other than locomotion, feeding, and defense when analyzing the possible evolutionary history of a group. Important features of an organism are associated with pair formation, reproduction, and raising offspring, all of which contribute strongly to the fitness value of individuals. Second, arboreal life usually favors the evolution of small size in animals. If the ancestral group was facultatively homoiothermic, the problem of excessive heat loss in smaller forms (Calder 1984) would have increased the need to evolve into obligatory homoiothermy. Third, if nesting was important in the evolution of avian homoiothermy, protobirds would have been inactive during incubation when they were supplying heat to their eggs; hence there was a need to evolve specialized homoiothermy and an insulating layer to lower the rate of heat production and thereby conserve energy stores. Lastly, homoiothermy almost certainly did not evolve under the action of selective agents associated with the active part of protobird life. If an animal is active, then it produces considerable heat and must lose heat; heat conservation and the need to produce internal heat would not be of primary concern.

If it can be argued successfully that homoiothermy is an essential prerequisite for flight, and if homoiothermy evolved in connection with the arboreal part of protobird life, then preflight protobirds were already in trees. Thus one can postulate strongly that flight probably evolved as locomotion from trees down to the ground.

The evolution of homoiothermy and of feathers is central to the explanation of avian flight. Any worker who wishes to argue for a terrestrial origin of avian flight must successfully explain the evolution of feathers and obligatory homoiothermy in terms of selective agents arising from the environmental demands of terrestrial life. In my opinion, none of the postulated terrestrial theories for the origin of birds and avian flight have dealt convincingly with these matters.

II. Body Size

Specialization for arboreal life would result in decreased size of the tetrapod to a small size, possible 500 gm or less, if the ancestral form was not already that small. Small size would confer favorable mass/surface area relationships for vertical climbing as well as for impacts should the animal fall or jump to the ground. A terrestrial, cursorial way of life generally favors an increase in size which would, up to a point, foster increased running speed and defense against predators. Smaller size is definitely advantageous for the origin of flight because of weight/surface relationships. Smaller size means that the animal can move through the air with smaller wings and lower air speed.

III. Three-Dimensional Orientation

Terrestrial locomotion takes place in a two-dimensional world. Flight, on the other hand, is rapid movement through three-dimensional space in which visual clues to the horizon are frequently lost and must be replaced with other clues.

Ground-dwelling species, such as man, operate in a two-dimensional world and react only within this reference frame. Humans must learn with strenuous training how to cope with a three-dimensional world. Even then, synthetic devices (e.g., artificial horizons) are required to provide information on the relationship to the horizontal. Three-dimensional orientation and its role for arboreal animals can be appreciated by examining the differences between dogs, which are strictly terrestrial, two-dimensional animals, and cats, which are not highly specialized arboreal creatures. Cats can cope far better with a three-dimensional world; for example, cats can reverse their body if needed, to land on their feet during a fall.

Three-dimensional orientation is an absolutely essential precondition for the evolution of flight of any sort, including primitive downward jumping and gliding. Three-dimensional orientation would not evolve in a ground-dwelling form, not even in a leaping organism. A long jump from the ground is still in the realm of the terrestrial, two-dimensional world. I know of no examples in which specialized, three-dimensional orientation has been demonstrated in a primary terrestrial vertebrate, one that did not have an immediate arboreal or flying ancestor. A three-dimensional orientation can, and almost always does, evolve in arboreal tetrapods, because life in trees is in a three-dimensional world. I doubt that three-dimensional orientation would evolve in cliff dwellers. These tetrapods still live in a two-dimensional world—one that is turned on its side.

IV. Bipedalism and the Hindlimb

All birds are bipedal, with the structure of the hindlimb and pelvis specialized for bipedal locomotion, or modified from this condition. These features are found, at least in a less specialized state, in *Archaeopteryx*. Earlier workers (e.g., Ostrom 1974) have successfully argued that the structure of the hindlimb, for example, the elongated tarsal bones, had evolved in association with terrestrial, bipedal locomotion. I fully concur with this conclusion. However, the pelvis of *Archaeopteryx* is not as large and the bones are not as fused together as in modern birds. And the synsacrum of *Archaeopteryx* is much smaller and far less fused than that of modern birds. Considerable question exists on whether the pubis is fully reversed in *Archaeopteryx*. All of these features suggest that bipedal locomotion in *Archaeopteryx* is not as specialized as in modern birds. This provides a real quandary because of the postulate that protobirds and *Archaeopteryx* are, at least, in part terrestrial, bipedal creatures, and probably hunted on the ground for their food. It is doubtful that *Archaeopteryx* ran quadrupedally on the ground.

Not all features of the hindlimbs can be associated with selective agents associated with ground-dwelling. The reversed hallux is one such feature. Without a doubt the hallux in *Archaeopteryx* is reversed, and its foot functioned as a grasping one. Specialized ground-dwelling birds tend to reduce and lose the reversed hallux. Very few primarily terrestrial tetrapods have evolved a reversed hallux. Apparently this reversal occurred in a few bipedal dinosaurs, although some disagreement still exists on this point. A reversed hallux results in a grasping foot, but it is difficult to conceive of aspects of terrestrial-dwelling that would have provided the selective agents needed for the evolution of a reversed hallux. Peters (1984) argues that the evolution of the hallux in protobirds was associated with the need to grasp food while tearing it to pieces before swallowing it. However, it is not clear why the food must be grasped by a foot using the reversed hallux, and not simply held against the ground or the perch as done by most modern birds (parrots are a notable exception).

Hence, the reversed hallux seen in *Archaeopteryx* and presumably present in protobirds can be best interpreted as a fea-

ture used for grasping branches during arboreal locomotion; hence the reversed hallux is associated with life in trees.

Objections have also been raised against an arboreal way of life for protobirds and *Archaeopteryx* because they could not have been good climbers, they could not have climbed up tree trunks, and arboreal life and climbing up tree trunks would have damaged the feathers on the forelimbs (e.g., Ostrom 1974; Peters 1984, 1985). The general assumption is that *Archaeopteryx* and protobirds must have climbed quadrupedally.

No strong support exists for these arguments, especially the assertion that climbing had to be quadrupedal. Bipedal modern birds do very well as arboreal creatures. They do not have to use their wings to move through trees. Other bipedal arboreal tetrapods exist, namely Tree Kangaroos (*Dendrolagus*) of New Guinea and Queensland. Bipedal forms (birds) can be excellent climbers on tree surfaces, climbing down as well as up trunks and beneath branches as well as on top of them, and these forms can climb with or without using the tail. Among birds, excellent climbers include the woodhoopoes (Phoeniculidae), woodpeckers (Picidae), woodcreepers (Dendrocolaptidae), several genera of ovenbirds (Furnariidae: *Xenops, Megaxenops, Pygarrhichas*), nuthatches (Sittidae, Neosittidae, *Hypositta* of the Vangidae), creepers (Certhiidae, Rhabdornithidae, Climacteridae), the Black and White Warbler (Mniotilda, Parulidae), and the Hawaiian Creeper (*Loxops,* Drepanididae). Although it is more reasonable to suggest that protobirds and *Archaeopteryx* were quadrupedal climbers, it is possible that they were bipedal climbers.

Two arguments have been advanced against *Archaeopteryx* being a quadrupedal climber: that it would damage the wing feathers, and that *Archaeopteryx* already possessed the specialized linkage system in the wing which extends and flexes the lower arm and hand simultaneously (Peters 1984, 1985). Damage to feathers when protobirds climbed up trees and crawled about among branches appears to have been greatly overemphasized. Some species of birds (e.g., mousebirds; Coliidae) spend their lives crawling about in bushes and trees without extensive damage to their feathers. Analysis of the wing linkage system is much more difficult. This system is central to normal functioning of the avian wing, not only in its folding and unfolding, but in maintaining proper position of the skeletal elements during flight (Peters 1985). A well-developed linkage system, as present in modern birds, would seriously impede or preclude quadrupedal climbing in *Archaeopteryx* (Peters 1985). But, none of the existing evidence argues for or against the presence of the wing linkage system in *Archaeopteryx,* and there is no reason why this system could not have evolved at a later stage of avian evolution after quadrupedal climbing was no longer necessary. The wing linkage system depends on the exact placement of the carpal bones, ligaments between them, and the morphology of muscles such as the M. extensor metacarpalis radialis. These details simply cannot be obtained from the available specimens of *Archaeopteryx;* hence the wing linkage system cannot be used as proof against quadrupedal climbing in *Archaeopteryx* or other protobirds.

Ostrom (1974) argued that the claws of the hind foot, including their sheaths, are relatively straight and possess small flexor tubercles as would be expected in terrestrial forms. He also claimed that the claws of the manus, which are long and sharp, served to catch prey and did not serve as climbing structures. These conclusions supported Ostrom's argument that *Archaeopteryx* was terrestrial, used its forelimbs to catch prey, and did not climb trees. At the recent *Archaeopteryx* conference in Eichstätt, Yalden (1985) agreed that the claws of the hindlimb were relatively straight, indicating terrestrial locomotion. However, he showed that the ventral projection of the claws from the wing and that the attachment of the flight feathers on the dorsal surface of the arm and hand bones are consistent with the use of the forelimb for climbing. Further, Yalden showed that toe claws of living predaceous birds are short and conical while those of climbing birds are long, curved, and narrow, with a thick dorsal rim that extends to the sharp tip of the claw. The claws of the manus of *Archaeopteryx* are exactly like the pedal claws of modern climbing birds. Yalden concluded that the whole structure and position of the digits of the hand and the morphology of their claws in *Archaeopteryx* are consistent with the hypothesis that *Archaeopteryx* was an arboreal bird that climbed quadrupedally up trees.

V. Trunk Shape and Structure

The shape of the trunk in *Archaeopteryx* is relatively elongated and slender compared to that in modern birds. Its rib cage and trunk vertebrae are of light construction and do not form a rigid trunk skeleton characteristic of modern birds. This is shown by the lack of fusion between trunk and sacral vertebrae (the latter do not form a synsacrum), the lack of uncinate processes on the ribs, the existence of gastralia (ventral ribs), the weak and unfused pelvic girdle, and the relatively weak pectoral girdle in *Archaeopteryx.* No definite sternum has been found.

In modern birds, the pelvic girdle must support the body and transmit forces to the ground when the animal is walking, running, etc. The pectoral girdle must support the body and transmit forces to the air when the animal is flying. The rigid trunk skeleton efficiently transmits the body weight to either the pelvic or the pectoral girdle depending on the form of locomotion. Lack of a rigid trunk skeleton and smaller, less-fused pectoral and pelvic girdles in *Archaeopteryx* decrease its ability to transmit locomotory forces and demonstrates rather strongly that the division of terrestrial and aerial locomotion was not yet specialized in this primitive bird. And it suggests that *Archaeopteryx* may not have been as specialized a bipedal runner as is generally believed. Rather, these morphological features indicate that quadrupedal locomotion (e.g., climbing in trees) may have been a significant part of *Archaeopteryx*'s locomotion.

VI. Wing and Tail Structure

The forelimb of *Archaeopteryx* is a reasonably specialized wing with a good aerodynamic surface formed by elongated flight feathers (Helms 1982). These feathers have an asymmetrical vane and provide the strongest support for the conclusion that *Archaeopteryx* possessed good flying ability (Feduccia and Tordoff 1979; Feduccia 1980). It was probably an excellent glider, with fine control of the direction and duration of the flight and fine control of landing. *Archaeopteryx* may have possessed some ability to flap, but if so it was a most rudimentary form of flapping flight.

Differences in interpretation still exist on the orientation of the glenoid fossa and the articulation of the humerus. However, little argument exists on the lack of the acrocoracoid process and of the triosseal canal which reverse the pull of the M. su-

pracoracoideus. Clearly the tendon of the M. supracoracoideus was not sufficiently reversed to insert on the dorsal aspect of the humerus in *Archaeopteryx* (Ostrom 1974, 1976*b*). I agree with Ostrom's conclusion that the M. supracoracoideus was still relatively weakly developed in *Archaeopteryx*, and that its pull contributed little to the upstroke of the wing. Elevation of the wing in *Archaeopteryx* may have been mainly by upward pressure of the air on it during flight. This passive elevation of the wing by air pressure presumably occurs only when flight is relatively rapid or when the animal is moving downward through the air.

Sy (1936) has shown that flight in pigeons is still possible after the tendon of the M. supracoracoideus has been cut but only level flight at best. A pigeon with a severed M. supracoracoideus cannot take off from the ground. Hence the lack of an acrocoracoid process and a triosseal canal and a presumably small, unspecialized M. supracoracoideus in *Archaeopteryx* argues against the possibility of its taking off from the ground as is necessary for terrestrial theories. At best, it would have to run very rapidly to achieve sufficient upward pressure on the wings to elevate them.

It could be argued that dorsal elevators raised the wing in *Archaeopteryx* (Olson and Feduccia 1979), and that the M. supracoracoideus only secondarily acquired the role as elevator of the wing. Quite clearly the dorsal elevators of the humerus had to raise the wing in the early stages of avian evolution, but no evidence exists for or against a claim that these muscles served for active elevation of the wing in strong flapping flight.

A number of earlier workers (de Beer 1954*a*) claimed that a small, ossified sternum was present in *Archaeopteryx*. However, most recent students of *Archaeopteryx* (Ostrom 1976*a*:137) concluded that no evidence exists for the presence of an ossified sternum. Certainly an ossified keel on the sternum did not exist in this bird. It is possible that a cartilaginous sternum was present in *Archaeopteryx*. It would be highly unlikely that the ventral ends of the ribs were not bound together by some cartilaginous elements. A cartilaginous sternum, if present, would be small as its posterior extension would be limited by the gastralia. *Archaeopteryx* possesses a well-developed furcula formed by fusion of the two clavicles at their medioventral ends. The dorsal ends of the furcula presumably articulated with the medial surface of the dorsal ends of the paired coracoids, but the details of the connection between the furcula and the scapula and coracoid are not known (Ostrom 1976*b*:7). Quite likely the furcula did not meet the anterior head of the scapula and hence did not form a triosseal canal. The coracoids are short, flat, and thin. All of these features taken together suggest that the avian flight muscles (the M. pectoralis and the M. supracoracoideus) were not as strongly developed in *Archaeopteryx* as in later birds. The paired coracoids are rather thin, which would have limited their strength as anticompressive braces needed for strong flight muscles. The short length of the coracoids would have limited the length of muscle fibers of the M. pectoralis which would have restricted the force output of these muscles as they shortened. The relatively weak, unreinforced rib cage and the lack of a bony sternum would have restricted the size (in cross-sectional area) of the M. pectoralis because of the reduced suitable area of origin of this muscle. It is quite possible that the M. pectoralis originated from a large portion of the rib cage and from the presumed cartilaginous sternum of *Archaeopteryx*, but the muscle fibers would have been thinly spread out over this area so that their total cross-sectional area, and hence the maximum force of the M. pectoralis, would have been small. Recent estimates that the size of the flight muscles in *Archaeopteryx* may be 15% of body weight appear to be too high. Moreover, serious problems exist if one uses only the weight or the mass of a muscle to estimate its functional properties (Bock 1974: 164–220). It is not possible to estimate force development of a muscle from its mass. The relationship between the power output required for locomotion and the power production (or the energy utilization) of muscles is quite complex and depends to a great extent on the structure of the muscle-bone system (whether the muscle is one or two-joint) and on how much the muscle shortens (Bock 1974).

Interpretations of the significance of the furcula for flight in *Archaeopteryx* and explanations of the origin of avian flight differ greatly. Although a furcula is not essential for avian flight (it is lacking in some strongly flying parrots, e.g., *Platycercus*), it seems resonable to postulate that a furcula was a prerequisite for the origin of avian flight. Olson and Feduccia (1979) argued that the presence of a strong furcula demonstrates that *Archaeopteryx* was an active flapping flier. They based their conclusion on claims that in modern birds most of the M. pectoralis arises from the furcular area (the furcula plus the coracoclavicular membrane), and that the main function of the ossified sternum and keel is to provide a site of origin for the M. supracoracoideus. But they provided no factual evidence to support these claims. Because they cited George and Berger (1966) as the source of myological details, and because these latter workers use the domestic pigeon (*Columba livia*) as the major basis for their descriptions, I dissected several specimens of this species to ascertain the exact nature of these muscle-bone relationships. In pigeons, and presumably in most birds, fibers of the M. pectoralis originate from the furcula and the coracoclavicular membrane. However, in pigeons, only a small portion of fibers of this muscle (about 5%, by my calculations) arises from this area. Most of the fibers of the M. pectoralis arise from the ventral third of the bony keel or from the lateral surface of the sternum and adjoining ribs (my observations agree with the description in George and Berger 1966:305–306). The M. supracoracoideus arises from the dorsal two-thirds of the keel and the adjoining medioventral surface of the sternum with some fibers originating from the ventral part of the coracoclavicular membrane. The bony keel evolved, at least in part, in association with increasing size of the M. pectoralis. Evolution of the bony sternum and of its ventrally projecting keel was most likely associated with two functional reasons. First, the bone would provide the needed strength for an anticompressive strut between the origin and insertion of the two massive flight muscles. Second, the bony sternum and keel would permit the muscles to contract asynchronously without excessive distortion of the whole pectoral girdle.

Ostrom (1976*b*:11) asked if the furcula in *Archaeopteryx* served as a transverse spacer between the shoulder sockets. Olson and Feduccia (1979) rejected this suggestion on the grounds that none of the ancestors of *Archaeopteryx* possessed such a spacer. But these ancestors were not flying animals (in the broadest sense) and would not need one. Ostrom's suggestion seems to be quite right. Atkins (1977) showed that the furcula in birds is part of a complex bone-ligament system that maintains proper

spacing between the two glenoid articulations. The furcula acts as a spring that prevents the dorsal heads of the coracoids from moving too far medially. Moreover, the furcula and associated ligaments prevent the dorsal heads of the coracoids from moving too far laterally. This spacing mechanism would have been necessary in the gliding stages of the evolution of avian flight. Hence, the presence of a well-developed furcula in *Archaeopteryx* supports the assumption that it was a flying animal but does not support the conclusion that it was an actively flapping flier; it could have been a glider.

A common but erroneous concept is that the difference between gliding and active powered flight is that only in the latter is muscular force needed. Muscles are needed in gliding to hold the wings out to the side so that they can act as airfoils and to hold the parts of the wing in proper position relative to each other. Moreover, muscular force is required to change the shape of the wing during flight, often against strong air pressure, and possibly to flap it at the end of a glide to lose speed during landing. The start of hypertrophy of the M. pectoralis and M. supracoracoideus and the modification of the muscles of the forelimb toward the condition found in actively flapping birds probably occurred during the gliding stages in the evolution of flight. The ventral position of the biceps tubercle (=acrocoracoid) in *Archaeopteryx* (Ostrom 1976*b*:10–12) suggests a poorly developed M. supracoracoideus that had only a small role in elevating the wing. These conditions would not have prevented gliding because upward air pressure could have elevated the wing.

Archaeopteryx possesses three unfused digits in its hand. As mentioned above, these digits bear sharp climbing-type claws. A still unresolved question is why protobirds lost two digits, regardless of the homology of the remaining digits (Hinchliffe and Hecht 1984). Lack of fusion of the digits into a solid carpometacarpus as seen in modern birds would have been a real disadvantage to any flying protobird, even if it were just gliding. As discussed above, the free digits would have been important in climbing. It has also been argued that they could have been used for catching or holding prey. Almost certainly the hand in *Archaeopteryx* could not have been used to catch prey because the drag from the flight feathers would have precluded rapid movement of the hand through the air. Holding prey was possible, but that use of the hand seems to have been at the cost of skeletal support for the primary feathers attaching to the hand. No adequate explanation for the free digits of the hand with their sharp claws has been provided by proponents of the terrestrial theory for the origin of avian flight.

Archaeopteryx agrees with reptiles and differs from modern birds in possessing a long tail. However, it differs from reptiles in possessing elongated feathers along the lateral edges of the tail, which form a broad airfoil. Although the feathered tail is well known, it has figured almost not at all in explanations of avian flight and has usually been passed off in some vague way as part of the aerodynamic surface. Peters and Gutmann (1985) pointed out that an essential condition for flight in tetrapods is that the center of mass of the animal must lie at or anterior to its center of lift. Otherwise the animal will be unstable in the air. They pointed out that in other gliding and flying tetrapods, the flight membrane stretches along the whole lateral edge of the trunk and often spans from the forelegs to the hindlegs. This elongated flight surface is structurally consistent with the quadrupedal locomotion of all other gliding or flying tetrapods. If bipedal protobirds evolved an aerodynamic surface only on the forelimbs, the center of lift would have been well anterior to their center of mass. This would have been especially true in the early stages in avian evolution before the flight muscles started to enlarge (i.e., at a stage subsequent to that characterized by *Archaeopteryx*). These early protobirds, being bipedal, possessed a relatively well developed pelvic appendage with large muscles, all of which would have shifted the center of mass posteriorly in the body, causing even greater balance problems when the animal was airborne. Peters and Gutmann argued quite correctly, that the evolution of a long airfoil along the tail provided a posterior lifting surface and thereby shifted the center of lift posteriorly to the center of mass. This long tail would have been retained, even though it provided a relatively flexible aerodynamic surface, until the flight muscles hypertrophied and the center of mass shifted forward. If the tail provided a reasonable amount of lift, even if inefficient, then it would have permitted a partial separation between the lifting surface and the oscillating surface of the wings, which provides thrust.

Evolution of Avian Flight

Explanation of the evolution of avian flight must show how all of the flight-related features evolved gradually and adaptively, always fitting together harmoniously, into a viable organism. For this discussion, I rely heavily on papers by Pennycuick (1975; this symposium), Rayner (1979, 1981, 1982, 1985*a, b*), Norberg (1985*a, b, c*), Clark (1977), Brackenbury (1984), Tucker (1938), and Brown (1951, 1963) for the essential nomological-deductive explanations on the physics of flight.

Flight is energetically the least expensive mode of tetrapod locomotion, be it gliding or active flapping flight. Tetrapods can cover a distance between two points using less energy by gliding from tree to tree and climbing up the second tree to a new launch site, than by climbing down the tree, running along the ground, and climbing up the second tree. Efficiency is increased by flattening the angle of the glide toward the horizontal to decrease the distance that the animal must climb up the tree.

The energy expense of flapping flight depends on the speed of flight. All of the above authors have shown that flapping flight is most costly at low speeds and again at high speeds; flight is most efficient at a medium speed. At low speeds and for hovering, active flapping flight is energetically costly. Hence, the type of flight that would be involved in the most rudimentary stages in the terrestrial origin of flight would be very costly. In the rudimentary stages of flapping flight in the arboreal origin of flight, the animal was already moving through the air at a reasonably moderate speed in a glide, and hence the cost of initial flapping would have been lower than the cost for terrestrial take-offs.

If avian flight started as gliding down from an elevated position in trees toward the ground, then gravity provided much of the force needed for movement. The animal did not have to provide muscular force to counteract the pull of gravity. The glide did not have to be a gradual drop from the launch site to the landing position. It could have been a rapid drop to build up the needed speed for efficient forward movement. Specializations to decrease the angle of descent of the glide would have allowed the animal to cover a longer horizontal distance for a given vertical height at take-off.

If flight had started from the ground up into the air, the animal would have had to move against the pull of gravity and provide muscular force to counter gravity. Hence large forces would have been required from the flight muscles. All features of the rib-cage and the pectoral skeleton of *Archaeopteryx* suggest that the M. pectoralis and the M. supracoracoideus were weakly developed—they were most likely smaller and produced relatively less force than those in modern birds that are almost flightless (e.g., Raikow 1985). Even if *Archaeopteryx* could have provided some forward thrust by flapping, it is doubtful that *Archaeopteryx*'s flight muscles were large enough to achieve upward flight from the ground. Such flight speeds would have been low, close to hovering, and hence energetically expensive. It has been suggested that the terrestrial origin of flight could have been a short flight at the end of a rapid run when the animal launched itself into the air with a leap and then glided or flapped for a short distance. Calculations suggest that the running speed needed to achieve take-off from the ground and a short flight would be excessively high for an animal the size of *Archaeopteryx* (Rayner 1985*c*).

The arboreal theory for the origin of avian flight assumes that an early stage was jumping or parachuting from trees to the ground, which led to gliding, and that gliding, as it became more and more specialized, led to active flapping flight. The initial jumping from trees may not have been accidental falls, but part of the normal descent of an arboreal tetrapod that was not specialized for head-first downward climbing, as seen today in most felids. Caple et al. (1983, 1984; Balda et al. 1985) have stated emphatically that gliding could not have evolved from a parachuting stage, that flapping flight could not have evolved from gliding, and hence that avian flight did not start from an elevated site down to the ground.

The controversy over the evolution of gliding from parachuting appears to be minor and may depend largely on definitions of parachuting and gliding. Most workers have used the term parachuting loosely, meaning a free fall in which the rate of descent is slowed by structures that increase air resistance. The angle of descent is rarely vertical because of wind, asymmetries in the air-resisting surfaces, etc. Caple et al. seem to restrict parachuting to strictly vertical drops and then argue that an animal requires more energy to glide than to parachute. As they assume that evolutionary changes cannot proceed from a condition requiring less energy to one needing more energy, gliding cannot evolve from parachuting. Their basic assumption is not justified (Bock 1980). I shall assume that all parachuting drops are at some angle of less than 90° to the horizontal, and that no real distinction separates primitive parachuting from gliding.

The more serious claim that flapping flight cannot evolve from an ancestral gliding stage is based on two major points. First is the belief that flapping would have evolved only to extend the length of the flight path, that is, to decrease the angle of descent more and more toward the horizontal. This assumes that the only selective advantage in flight, either gliding or flapping, is increase in the length of the flight path. Second, Caple et al. argued that any action that decreases lift would reduce the length of the flight path. They stated that maximum lift occurs when the wings are held horizontally and that flapping would involve the wings moving away from the horizontal—hence, lift would decrease. They claimed further that in the earliest stages of flapping flight evolution from a gliding animal, the loss of lift and of the distance covered was greater than the increase of forward thrust and of distance gained from flapping. These arguments suffer from several serious defects.

Flapping during a glide can have several adaptive advantages other than to increase the length of the flight path. It could control flight direction, it could slow the flight and thus decrease the flight path if desired, or it could brake the animal in the air just before landing. All of these actions could have advantages and could provide the basis for the improvement of flapping in a gliding animal.

While it is true that wings held horizontally would provide the greatest lift, no evidence exists that protobirds and *Archaeopteryx* held their wings in a flat plane. A number of modern soaring birds, or birds that intersperse flapping with short glides such as domestic pigeons, glide or soar with uplifted wings, for example, held in a dihedral. This arrangement of wings seems to be advantageous in unsteady winds or in turbulent air. If protobirds glided with wings held dihedrally, then their movement during a flap might not reduce the overall lift.

The avian wing is divided into two parts. An inner part comprised mainly of the secondaries attaching to the ulna is the lift-generating portion. The other part consisting mainly of the primaries attaching to the hand is the thrust-producing portion of the wing. These two parts are relatively separate. There is no reason why the wing in *Archaeopteryx* could not have been similarly separated, permitting the evolution of a distal, thrust-producing part without decreasing the lift of the inner, lift-producing segment. Moreover, little attention has been given to the lift production of the tail, which would not have changed as the wings were flapped.

Lastly, Rayner (1985*b*) and Norberg (1985*b*) have shown that evolution of flapping flight does not decrease the length of the flight path compared to that of a glide. Instead, the flight path becomes shallower and therefore longer. Efficiency of gliding and flapping flight can be compared by calculating the energy required by an animal traveling from a certain height in one tree to an equal height in another tree. Gliding would be at a steeper angle than flapping flight; hence the gliding animal would have to climb a greater distance up the second tree than the flying animal. Rayner has shown that the cost of transportation is smaller for flapping flight than for gliding and the required longer climb. The difference in energy cost becomes greater as the angle of the glide becomes steeper, and the energy cost reaches its maximum when the animal climbs down the first tree, runs to the second tree, and climbs up it.

Thus it is reasonable to conclude that (a) gravity provided much or all of the force needed for the initial stages of flight (gliding), (b) parachuting and gliding preceded active flapping flight, (c) flapping could have started for reasons other than to increase the length of the flight path, and (d) even with rudimentary flapping, no evidence exists to prove that flapping decreased the length of the flight path or made flight less efficient.

Comparison of Terrestrial and Arboreal Theories for the Origin of Avian Flight

Having discussed some of the available factual evidence and some theoretical aspects of the physics and physiology of essential features associated with avian flight, it is now necessary

to state the rival theories, compare them, and test them against this evidence.

I. Pseudophylogenies and Analogous Forms

A historical-narrative explanation of any particular major evolutionary event depends on the establishment of a chronological sequence of intermediate forms—a procedure used ever since Darwin (Bock 1979:58–59). The exact nature of the intermediate forms is critical. In general, each will be a mosaic of ancestral, descendant, and intermediate characters (de Beer 1954*b*). Moreover, these pseudophylogenies must have several properties.

(1) Each level sets the stage for the next evolutionary step. All evolutionary modifications at any point in the pseudophylogeny must be based on the set of known and postulated characteristics of the organism existing at that time.

(2) Each successive evolutionary step must be small, that is, at the level of differences between species or the level of changes observed by population geneticists and by animal and plant breeders. The successive small changes are additive, forming a gradual pattern of major modification. Large, abrupt steps, or saltations, are not acceptable.

(3) The organism at each stage must constitute a functional and adaptive whole. All of the features of the organism must fit together morphologically and physiologically. For example, obligatory homoiothermy cannot evolve in small tetrapods in the absence of an outer insulating layer. And the organism must interact successfully with all of the environmental demands at each stage in the evolutionary sequence.

(4) Each step must be adaptive in the sense that the features of the organism being considered must be adaptive in terms of the selective agents acting on that organism. And evolutionary change from one stage to the next must be adaptive.

(5) As far as possible, each stage in the pseudophylogeny should be represented by an analogous known organism. It must be emphasized that the analogous forms of the pseudophylogeny need not be, and often are not, closely related to each other in any real phylogenetic sense. For example, tree kangaroos (Dendrolagus) serve as an analogous bipedal arboreal form, and flying squirrels (*Glaucomys*) or gliding possums (*Schoiobates*) as analogues for the parachuting and gliding stages.

If a pseudophylogeny for the explanation of a particular major evolutionary event is established with no known analogous forms, then that pseudophylogeny is suspect. In contrast, analogous organisms existing for most or all stages in a pseudophylogeny give considerable confidence in that sequence. It must be stressed that the assembly of a complete set of analogous organisms is not proof or confirmation of a narrative explanation for a particular evolutionary change and that lack of analogous forms does not constitute disproof. After all, unique major evolutionary changes exist for which no analogous forms will be found. No analogous intermediate forms can be found for the evolution of avian feathers except for the initial elongation of the reptilian scale. And yet, the pseudophylogeny for the evolution of avian feathers postulated by Regal (1975) is convincing.

II. Terrestrial Theories for Avian Flight

These theories postulate that flight originated from the ground up into the air against the pull of gravity. They can be characterized as running terrestrial (Nopcsa 1907, 1923), insect net (Ostrom 1976*b*, 1979), and leaping (Caple et al. 1983, 1984) theories. Their proponents have neither provided good pseudophylogenies nor supplied analogous known organisms for several important stages in the sequence of changes. Moreover, these theories have a very large evolutionary step between the last preflight stage (e.g., a jumping organism) and the active flapping flight stage. Too many interrelated features required for flight (e.g., three-dimensional orientation, obligatory homoiothermy) are inadequately discussed.

The terrestrial theories do not consider adequately the integrated evolution of all avian features, or even those closely associated with flight, for example, those features known or presumed to occur in *Archaeopteryx*. These include the feathered tail; obligatory homoiothermy; the reversed hallux; the structure of claws on the hand; the elongated, flexible trunk skeleton; and the existence of three-dimensional orientation.

The terrestrial theories usually disagree with the idea that protobirds lived in trees. They argue that the claws of the hand are not suitable for climbing, that quadrupedal climbing would damage the flight feathers, and that early stages of leaping and gliding could not be from tree to tree because of orientation problems. The first point has been shown to be invalid by Yalden (1985). The second is not supported by observations of young hoatzins (*Opisthocomus*) and mousebirds (*Colius*) climbing about in branches that would damage the wing feathers far more than quadrupedal climbing on trunks. The earliest leaps need not have been long ones from tree to tree; they could have been from trees to the ground. Or the initial leaps could have been very short ones that did not require any midair readjustment of the flight path.

The terrestrial running theory of Nopcsa (1907, 1923), postulates that the evolution of wings and of flapping would have provided additional forward thrust that would have increased the speed of locomotion. As flapping increased, the animal would have been lifted into the air. This theory is based on the fact that a number of large birds, both land and aquatic, must propel themselves by their feet for a distance until they attain sufficient forward speed to be able to take-off. These birds flap their wings vigorously as they run along. In all of these cases the birds run as part of the needed take-off for flight; they do not use their wings to increase running speed. The use of wings to increase running speed occurs rarely, if at all, in present day birds. Outstretched wings increase drag on the running animal so that additional force is needed just to overcome this additional resistance. Further, the lift created by flapping the wings counters the pull of gravity in the bird and hence decreases the downwardly directed contact force between the animal and the ground. Friction between the foot and the ground decreases, traction decreases, and the animal cannot achieve as much forward thrust with its feet by running. These factors hold true for a modern bird running during take-off, but these birds have well-developed wings that can take over forward thrust as soon as the necessary speed is achieved. If a running protobird needed to increase its speed, the most feasible evolutionary change would be to improve the capacities of the hindlimb, either by enlarging the muscles or lengthening the limb bones, or by both. Attempts to increase running speed by flapping the forelimb would be disadvantageous as they would increase air resistance and would decrease traction.

Ostrom (1974:30–31, 1976*b*) showed that Nopcsa's running theory was invalid for the reasons just presented, and postulated that the forelimb feathers elongated and that flapping developed in connection with feeding activities. Ostrom contended that feathered forelimbs evolved as an insect net for catching prey. This explanation for the origin of avian flight has several serious flaws. As has been pointed out by many workers, if the forelimb feathers evolved as an insect net, they must have had an open structure to permit air to pass through, but not the food items to be trapped. A continuous surface of wing feathers, as seen in *Archaeopteryx,* would be essential for a suitable aerodynamic surface, but would not work as a net to trap prey. Furthermore, this theory does not account for the structure of the feathered tail. These objections undermine the insect-net or predation explanation for the origin of flight, which was given up several years ago by its original proposer.

Most recently, Caple et al. (1983, 1984; Balda et al. 1985) argued quite correctly that little attention has been given to the question of control of body orientation of an animal during a leap and that the feathered wing and flapping evolved as adaptations to control body orientation during a leap and in landing. They stated that these features would increase the distance of the leap and therefore increase the ability to capture insect prey. They then concluded that the evolution of avian flight began with active flapping flight and never passed through a gliding evolutionary stage. Evolution of the wing, including flight feathers, started from the distal end of the forelimb with the primaries evolving before the secondaries. This theory assumes a small animal with a rigid lightweight body. The leaping explanation for the origin of avian flight states emphatically that "Pro-avis developed the capabilities for powered flight from a bipedal cursorial habit." (Caple et al. 1983:475). No comments are made on whether protobirds were strictly terrestrial or spent part of their lives in trees. Moreover, this explanation is silent on points such as the evolution of feathers, obligatory homoiothermy, the reversed hallux, the structure of claws on the hand, three-dimensional orientation, and the structure of the feathered tail. (A brief statement on tail structure by Caple et al. 1983: 469 is not adequate). Lastly, the evolutionary step from leaping, assisted by flapping, to fully developed flapping flight is a very large one that is dealt with only by stating that "The result of these collected changes [for increasing the leap to capture prey and landing] will lead to powered flight." (Caple et al. 1983: 473).

Proponents of the leaping terrestrial theory have not provided a suitable pseudophylogeny for their explanation, and they have included a very large evolutionary step from leaping to powered flight. They do not cite analogous known organisms for stages in the needed pseudophylogeny except for the initial running and leaping stages. I know of no small tetrapods about the size of *Archaeopteryx* that are primarily terrestrial (e.g., not flying-running forms, or secondarily flightless or degenerate flying forms) and use their forelimbs for balance during fast running or during a leap. And I know of none using the forelimbs as flapping structures to provide forward thrust to increase the length of its leap. Control of landing on the ground appears to be of minimal importance during a leap for food. Many tetrapods using long leaps to capture food in the air land most awkwardly. And even in modern birds, the young know how to fly instinctively in that they can take off and fly with little or no training, but they must learn how to land.

My objections are not directed against the physical analyses by Caple et al. (1983) of features serving to stabilize an animal during an airborne trajectory, which are nomological-deductive explanations, but against the accompanying historical-narrative explanation for the origin of avian flight. The approach used by Caple et al. (1983) of arguing for the morphology, functional properties, and biological roles of possible intermediate forms from a strictly mechanical analysis is dangerous at best and generally invalid. This approach overlooks the need to base phylogenetic reconstructions on the features of the preceding stage (e.g., Gutmann 1977, 1981) and on the need to analyze the functional and adaptive aspects of individual features in a holistic fashion. The latter requirements have been demonstrated nicely by LaBarbera (1983) who showed that the reason wheels (rotating locomotory structures) have not evolved in organisms was not solely or mainly because of morphological and/or developmental constraints, but because of adaptational limitations. The points raised by LaBarbera apply equally well to the arguments of the physics of leaping and gliding presented by Caple et al. (1983).

Before leaving the terrestrial theories for the origin of avian flight, one general objection to these explanations must be pointed out because it is based on available empirical evidence from *Archaeopteryx,* not theoretical analyses or arguments from features presumed to be present in protobirds and in *Archaeopteryx.* All of these terrestrial theories depend absolutely on protobirds and *Archaeopteryx* being specialized bipedal, cursorial, terrestrial organisms. They are considered to be not only bipedal and terrestrial, but also highly specialized for cursorial locomotion, regardless of their presumed abilities to glide or fly actively with flaps of their forelimbs. Thus, these theories predict that protobirds and *Archaeopteryx* must have pelvic girdles, hindlimbs, and trunk skeletons that are well adapted to the selective demands for terrestrial cursorial locomotion; these features should be at least as specialized in *Archaeopteryx* as in modern birds. Even a cursory glance at the structure of the trunk skeleton (rib cage and thoracic vertebrae), the synsacrum, the pelvic girdle, and the hindlimb of *Archaeopteryx* demonstrates that all of these features are much less specialized (see above) for cursorial bipedal locomotion than are the same features in modern birds. I do not disagree with the conclusion that *Archaeopteryx* and protobirds were bipedal terrestrial creatures, but the available evidence simply does not support the conclusion that they were specialized, rapidly running and/or leaping terrestrial animals. There is no reason why these features of the pelvic girdle and hindlimb should have become better adapted to the selective demands associated with bipedal cursorial locomotion in modern, fully flying birds than in a specialized bipedal, cursorial, ancestral *Archaeopteryx.* It is difficult to think of selective demands associated with arboreal life or with flight which would favor the evolution of the hindlimb and pelvic features of modern birds if protobirds and *Archaeopteryx* were already well adapted to the demands of specialized cursorial locomotion. It is highly doubtful that these specialized features of the hindlimb and pelvic girdle in modern birds are adaptations to demands associated with landing—a sort of shock absorber. Birds use their wings to brake their flight just prior to

landing. The hindlimbs and pelvic girdle are far less developed (specialized) in *Archaeopteryx* than in those groups of modern birds (swifts, hummingbirds, nightjars, man-of-war birds) that never use the hindlimb for locomotion, but only for perching. This evidence is fatal to all terrestrial theories for the origin of avian flight that are based on a specialized cursorial protobird. Moreover unless empirical evidence becomes available and shows that protobirds (e.g., *Archaeopteryx* or some yet undiscovered fossils) were indeed specialized bipedal, cursorial animals, any proposed terrestrial theory for the origin of avian flight cannot be based on the premise of specialized bipedal, cursorial locomotion in the protobird.

III. Arboreal Theories for Avian Flight

A number of arboreal theories of the origin of avian flight exist, and they differ in several critical aspects. Many are silent on whether protobirds lived only in trees or partly in trees and partly on the ground. The explanations for the evolution of feathers also differ significantly: were they originally for regulation of heat flow and secondarily for flight, or originally for flight and secondarily as an insulating layer? Differences in explanations for the origin of feathers are reflected in the divergent views on the evolution of obligatory homoiothermy—did it have to evolve prior to the origin of flight, did it evolve after the development of active flapping flight, or did obligatory homoiothermy and flight evolve independently of one another. The significance of these differences in arboreal theories for avian flight, especially those concerning the evolution of feathers and obligatory homoiothermy, cannot be over emphasized. In the arboreal theory that I advocate, protobirds lived partly on the ground and partly in trees, and homoiothermy and feathers (originally for reduction of heat flow) evolved prior to the first stages of flight.

A rather complete pseudophylogeny can be established (Bock 1965) with many intermediate stages, none of which represent an unreasonably large evolutionary jump, and with known analogous forms for almost all stages. The only steps that lack known analogues are those between specialized gliding and active flapping flight. A number of birds exist with vestigial flight, but these are not valid analogues for the early stages of flapping flight.

The ancestral organism (initial condition) was a small, terrestrial, diurnal reptile. It may have been quadrupedal or bipedal; the difference does not matter at this point. It was not a specialized bipedal, cursorial animal. And it probably fed on animal prey, but that is not certain. Nor can anything be said about the exact nature of its prey and how the prey was captured.

The first stage was to become arboreal. This was most likely for escape, hiding, resting, sleeping overnight, and eventually for breeding; trees were used as a place to put the nest while the eggs were being incubated and the young being raised until they reached adult size. This stage can easily be subdivided into a number of small steps. Features that evolved as adaptations to the selective demands of arboreal life include the reversible hallux; the sharp, curved claws of the manus; feathers to regulate heat flow; obligatory homoiothermy; and three-dimensional orientation. (I include only features related to the evolution of flight and do not consider others such as reduction in the olfactory sense, probable improvement in vision and hearing, etc.) Trees were almost certainly not used as a feeding site until well into the evolution of birds and perhaps only after the evolution of flapping flight.

Locomotion in trees was presumably by quadrupedal climbing up trunks and major branches and by quadrupedal crawling or walking on branches. The animals, as they became more specialized, could move from tree to tree by crawling out along branches where they meet or by jumping short distances between branches of neighboring trees much in the same way as do present day squirrels. A more difficult problem, but one that has not been considered to my knowledge, is how protobirds climbed down trees. Unspecialized quadrupedal arboreal tetrapods, for example cats, can readily climb up trees, but can only poorly climb down trees. Specializations such as the ability to reverse the direction of the limbs and feet when descending headfirst, as seen in squirrels, are needed for efficient downward climbing. No indication exists as to whether such specializations ever appeared in the early evolution of protobirds. In the presumed absence of such downward climbing specializations in protobirds, it would have been advantageous for these animals to descend from trees by jumping down (jumping is the most energy-efficient way to descend from trees [Stewart 1985]) and to evolve features which would have slowed the speed in the free fall and hence decreased the force of impact on the ground (see Stewart 1985, for plopping behavior in arboreal frogs). Free falls need not have been originally from high in trees, but from partway down the trunk. Any feature that could have served as a parachuting device would have been adaptive. These would include holding the body horizontally with outstretched limbs and tail, and increasing the surface area of these appendages by lengthening feathers along the margins.

During these early arboreal stages, protobirds still fed on the ground. At some time, whether before or after taking to the trees, these animals evolved bipedal terrestrial locomotion. The selective advantages for bipedal locomotion are not clear, but I would concur with those workers (e.g., Ostrom) who argue that bipedal locomotion evolved in response to demands of terrestrial life. Bipedal locomotion is presumed to be relatively slow, not a specialized rapid cursorial type or an active leaping one, until after the *Archaeopteryx* stage.

Evolution of bipedal locomotion would have had serious consequences for arboreal locomotion. These now bipedal protobirds could still have climbed up trees, probably quadrupedally but possibly even bipedally, and moved around on branches. And they still could have moved from tree to tree by crawling along the branches and leaping over short gaps. But bipedal locomotion would have made descent from trees by climbing down even more difficult. Crawling backwards down tree trunks would have become difficult to impossible once elongated feathers started to evolve along the lateral margins of the tail and posterior edge of the forelimbs because of damage to these feathers. Few specialized climbing birds are able to descend tree trunks, head-first or otherwise.

At this point, evolution of methods for descending trees other than climbing down them would have been essential. The most obvious ones would be jumping down—free fall (parachuting) or gliding. Any features that would have decreased the speed of the descent and thus the impact force of the ground would have

been advantageous. Analogous tetrapods include the tree frog, *Rhacophorus rheinhardtii,* and the Borneo snake, *Chrysopelea* (Lull 1906; Rayner 1981; Norberg 1985*a;* Stewart 1985). Presumably none of these parachuting falls are vertical drops but are, at the minimum, glides with large angles of descent. The evolution of features to improve free falls from trees in protobirds is critical because these animals would have had to reach the ground to feed. If the nest were placed in trees and the parents were feeding their young, this would have involved many round trips per day to the ground and back again.

The evolution of gliding adaptations would have followed rapidly because they would have increased the ability to descend from trees, would have improved the efficiency of horizontal locomotion away from the tree to feeding sites, and so on. Evolution from an unspecialized, free-falling animal to a highly specialized, gliding form can be divided into a large number of small steps; and countless analogous forms can be cited (Lull 1906; Rayner 1981; Stewart 1985). As has been pointed out by every author analyzing the efficiency of tetrapod locomotion, gliding from tree to tree or from the tree to the ground and climbing up the next tree to gain height for the next glide requires far less energy than running along the ground. Any evolutionary changes that improve the glide (e.g., flattening the glide path) further reduce the energy needed for covering horizontal distances.

Specialization of gliding involves not only increase in distance of the glide, but improvement of maneuverability, of braking during flight and just before landing, and of other abilities, all of which have evolved in various specialized gliders. Such specializations in protobirds include improvement in the shape of the wing surface and in the structure of individual flight feathers, increase in the size of the flight muscles and other pectoral muscles (e.g., force development and duration of contraction before fatiguing, and strengthening of the pectoral skeleton.) These specializations include active movements of the wings in some flapping mode, but these movements need not always provide forward thrust. Quite probably, initial flapping movements of the wings impeded forward movement and braked the animal either to land or to shorten the flight. Selective advantages for specialization of gliding and for the origins of flapping (not flapping flight) are many. Successful gliding in tetrapods is not simply launching into a straight glide. It is control of the whole glide from start to finish. The animal may have to avoid obstacles in its path, correct for wind, change the landing site at the last minute, etc.

Once the animal has evolved the ability to flap its wings, flapping can be used when needed to provide additional forward thrust in the air and thereby extend the flight path. At first, the flight path would be increased by decreasing the angle of descent and only later by actually gaining elevation and hence achieving active powered flight.

The evolutionary change from simple gliding to advanced, controlled gliding and then to active flapping flight can be divided into a number of small steps. Flapping may have originated as a means of maneuvering and/or of braking and may have evolved under the control of selective agents associated with these actions. Analogous forms exist for the steps of improved gliding, but no tetrapod analogues can be pointed to as representatives of the earliest stages of active flapping flight.

It seems reasonable to postulate that early flapping flight served as a means of getting from trees down to the ground and of covering horizontal distances rapidly and efficiently. Only after flapping flight became somewhat specialized could it be used to move from the ground up into trees and after that as a means of hunting and/or capturing food. Contrary to the claims of some workers favoring the terrestrial origin of avian flight (e.g., Padian 1982*a:*11), true fliers such as birds do not use flight in all of their life activity but often only in very restricted ways. And no sharp separation exists between gliders and true fliers.

Caple et al. claim that: "No modern gliding animal can even approach the conditions necessary for active flapping flight" (1983:475); and that:

> There is no compelling aerodynamic reason for the gliders to change. They are well adapted to their forest niche. They have minimized their energy expenditure in traveling with a gliding mode which does not interfere with surface movement.
>
> Rather than arboreal gliders being thought of as intermediate forms in the evolution of flight, they should be considered for what they are. It appears that the better their gliding capabilities, the less need there is (and the more difficult it is) to become a powerful flyer. Birds can and do imitate gliders; gliders do not imitate birds. Gliders are not intermediate flyers" (1984:38).

These claims are evolutionarily naive at best. They imply that gliders are evolutionary dead ends and are absolutely unable to improve their flying abilities from gliding to active flapping fliers regardless of the environmental conditions and the resulting selective demands. The demonstrations by Rayner (1985*b*) and by Norberg (1985*b*) that flapping flight requires less energy for horizontal locomotion from point to point than gliding counter the claims by Caple et al.

I feel that the arboreal explanation for the evolution of avian flight offered above fits the requirements of historical-narrative explanations for evolutionary changes. This explanation is supported by the empirical evidence available from *Archaeopteryx* and by nomological-deductive arguments from the physics of flight. I know of no empirical evidence or valid theoretical arguments that argue strongly against it.

IV. The Archaeopteryx Stage

The morphology of *Archaeopteryx* is consistent with the conclusion that it spent some of its time on the ground as a bipedal running animal. But it was probably not a specialized cursorial and/or leaping form. Its relatively small, weak and unfused pelvic girdle and synsacrum suggests that *Archaeopteryx* was slow moving during terrestrial locomotion. It also lived in trees part of the time as indicated by the reversed hallux and the curved, sharp claws on the three fingers of the hand. *Archaeopteryx* was clearly a flying bird, as shown by its wing with long flight feathers, which have asymmetrical vanes, and the long feathers along the lateral borders of its tail. Almost certainly *Archaeopteryx* was not an active flapping flier because the bones of the pectoral girdle are small and relatively weak (short coracoid, unossified sternum, no sternal keel). If *Archaeopteryx* flapped its wings, it probably did so to control the gliding flight path or to achieve a rudimentary flapping flight at best. It is highly doubtful that *Archaeopteryx* was the powered flier claimed by a number of workers, including some proponents of the arboreal theory.

A large number of avian features evolved after the *Archaeopteryx* stage and presumably after fully powered flight was achieved. These include fusion of the free, hand digits into the

avian carpometacarpus, enlargement and ossification of the sternum, appearance of the keel, elongation and strengthening of the coracoid with modification of its dorsal end to form the triosseal canal, appearance of uncinate processes on the ribs, increased rigidity of the trunk skeleton, increase in size and fusion of the pelvis and synsacrum, complete fusion of the tarsometatarsus, and shortening of the caudal vertebra into the pygostyle to which the tail feathers attach. The evolutionary change of most of these features from the condition seen in *Archaeopteryx* to that in modern birds was the direct consequence of the evolution of active flapping flight. Although these are major modifications, it seems likely that they could have occurred rapidly once avian powered flight evolved. The estimated ten million years separating *Archaeopteryx* from *Ambiortus* (the oldest known keeled bird, Kurochkin 1982, 1985) or from *Gansus* (Hou and Liu 1984) allow, in my opinion, more than sufficient time for the evolution of powered flight, an ossified sternum with a well-developed keel, and the rest of the changes mentioned above. It is not known if most of these changes took place prior to the appearance of *Ambiortus* and *Gansus* because most of these features are not preserved.

Conclusions

The evidence presented in this paper strongly supports the arboreal theory for the evolution of avian flight as the only viable explanation at this time. Moreover, the arboreal theory is so strongly corroborated that to reject it will require serious discussion and powerful rebuttal of the theory's central foundations. This is not to claim that future analyses will never find the arboreal theory wanting, but only that the necessary evidence and arguments must be persuasive. Even if the arboreal theory for the evolution of avian flight is convincing and becomes generally accepted, it cannot be applied simply to the evolution of flight in pterosaurs and in bats. The morphology of these other groups of flying tetrapods differs greatly from that of birds; it appears most reasonable that there will be significant differences in the explanations for the evolution of flight in each group.

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The Cursorial Origin of Avian Flight

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Introduction

For more than a century naturalists and scholars have speculated about the origin of bird flight, and that is the primary subject of this symposium. I would like to thank the Fellows of the California Academy of Sciences, the Pacific Division of the American Association for the Advancement of Science, and Dr. Luis Baptista of the California Academy of Sciences for inviting me to contribute to this symposium. I would also like to thank my colleagues for their participation and contributions to a most intriguing question—How or why did birds learn to fly?

These same questions were addressed three months after this symposium, September 11–15, 1984, at the International *Archaeopteryx* Conference in Eichstätt, West Germany. The paper that follows has not been modified to incorporate any of the relevant issues that were presented at Eichstätt. It is published here essentially as it was presented in San Francisco in June of 1984.

To summarize briefly, there are two principal hypotheses on how bird flight evolved. These may be expressed simply as the "from the trees down" hypothesis—the long widely accepted arboreal theory—or the "from the ground up" hypothesis—the often ridiculed cursorial theory. Allow me to elaborate a little about each of these theories and present some of the history behind them. Then I will make my case for the "ground up" theory.

The Arboreal Theory

Othniel Marsh (1880:189; 1881) of Yale College first suggested that:

> [The] power of flight probably originated among small arboreal forms of reptilian birds. How this may have commenced, we have an indication in the flight of *Galeopithecus*, flying squirrels *Pteromys*, the flying lizard (*Draco*) and the flying tree frog (*Rhacophorus*). In the early arboreal birds which jumped from branch to branch, even rudimentary feathers on the forelimb would be an advantage as they would tend to lengthen a downward leap or break the force of a fall.

This very logical and simple explanation was skillfully elaborated by my friendly adversary Walter Bock who (I believe) still firmly believes that birds first learned to fly by "falling out of trees." The logic of the arboreal scenario is difficult to refute: Stage 1) an ancestral ground-dwelling quadrupedal reptile (sometimes identified as a "thecodont" or primitive archosaur); Stage 2) a bipedal ground-dweller (an advanced thecodont); Stage 3) a bipedal tree-climber; Stage 4) a bipedal tree-dweller; Stage 5) leaping between branches; Stage 6) leaping between trees; Stage 7) parachuting between perches; Stage 8) gliding from high perches to lower trees or the ground; Stage 9) active flapping, powered flight.

Walter Bock's 1965 seminal contribution showed that a rational and logical explanation based on the accumulation of numerous microevolutionary changes over many generations could account for the seemingly macroevolutionary differences between a four-legged ancestor confined to a ground-living existence and our high-flying feathered friends. The significance of his contribution is that it showed that each intermediate stage on the way to bird flight could have been fully adapted to an incipient-flight, transitional life style. Selective pressures might have induced additional changes, all subject to further selective changes as a protobird ancestry gradually became equipped with the anatomical and physiological equipment necessary for eventual powered flight. The critical and most important point of this arboreal model, though, is that in order to fly protobirds first had to be able to climb. It is not clear from the limited available evidence (the specimens of *Archaeopteryx*) whether that was possible, but without an elevated perch, flight could not have happened by way of this hypothesis (but see Pennycuick, this volume).

In due course, we will consider the anatomical design of modern birds and especially that of the oldest known bird, *Archaeopteryx*. From these data, it is doubtful that climbing skills were part of the repertoire of primitive birds, or even of early bird ancestors. The clawed hands of *Archaeopteryx* might have been adapted for climbing, but there is disagreement on this.

The Cursorial Theory

This is the so-called "ground up" theory of flight origin first proposed by Samuel Wendell Williston (1879:459), also of Yale College.

> It is not difficult to understand how the fore legs of a [bipedal] dinosaur might have been changed to wings. During the great extent of time in the Triassic, in which we have scanty records, there may have been a gradual lengthening of the outer fingers and greater development of the scales, thus aiding the animal in running. The further change to feathers would have been easy. The wings must first have been used in running, next in leaping and descending from heights, and, finally, in soaring.

Williston gave no other details to support this novel and seemingly impossible "bootstrap" origin of bird flight. But in 1907 and in 1923, Baron Franz Nopcsa of Hungary published two papers on the origin of flight in which he gave somewhat more detailed accounts. In effect, the "protowing," according to Nopcsa's model, developed as a propeller—not a wing—adding thrust to the powerful running legs of a bipedal "proavis":

> . . we may quite well suppose that birds originated from bipedal long-tailed cursorial reptiles which during running oared along in the air by flapping their free anterior extremities. (Nopcsa 1907:234).

His idea, presumably, was that the free-flailing forelimbs of a running biped would become longer over many generations, and that the surface area of those forelimbs would be increased by enlargement of scales or "protofeathers." Thus, arm flapping would add thrust and augment the running speed of the hind limbs. It is not surprising that Nopcsa's theory was severely criticized and soon rejected, because the minuscule amount of additional thrust produced by those earliest enlarged "protofeathers" could hardly have produced any measurable selective

FIGURE 1. The solitary feather imprint reported by von Meyer in 1861. It is now in the collection of the Humboldt Museum fur Naturkunde in East Berlin. Scale units are mm. (From Ostrom 1976*b*.)

advantage. Consequently, the arboreal theory of flight origin has prevailed—at least until recently.

The Evidence

It is clear from the diverse anatomical designs among past and present vertebrate fliers that flight evolved several different times, by very different pathways. What makes avian flight particularly fascinating is that birds are the only fliers that are bipedal rather than quadrupedal. (Pterosaurs, or flying reptiles, may have been bipedal too, although the evidence is scanty and subject to other interpretations. For discussion of this, see Padian 1980, 1983.) The avian flight apparatus does not involve the hindlimbs, which are independent and well designed for alternative modes of nonflight locomotion—walking, running, or paddling. With the possible exception of some pterosaurs, no other flying vertebrate has developed two completely independent modes of locomotion. In my mind, that clearly indicates that bird ancestors were bipedal cursors long before flight ever developed. Furthermore, that restriction seems to me to diminish the probability of any bipedal climbing stage—and climbing is a necessity for the arboreal theory of flight origins. Aside from birds, virtually all other living arborealists are quadrupeds. The fact that many birds today are arboreal is quite immaterial because that could be (and probably is) a secondary habit that arose only *after* powered flight had been achieved by birds.

Since modern birds are the end products of a long evolutionary history, they are of little value in pondering the earliest stages of avian flight development. To explore that remarkable achievement of some 150 million years ago, we must rely on ancient evidence—the half-dozen specimens of *Archaeopteryx* from the late Jurassic rocks of Germany that represent a stage in bird evolution very close to the beginnings of flight. Here is that evidence.

1) A single feather (Fig. 1), found in 1861, now in the Humboldt Museum of East Berlin. The counterpart of this is in the State Collections of Bavaria in Munich, West Germany.

2) The London specimen (Fig. 2), found in 1861, which first associated fossil feather impressions with skeletal remains—described by some as just a feathered reptile.

3) The famed Berlin specimen (Fig. 3), found in 1877—perhaps the most famous of all scientific specimens because it has been cited and illustrated so many times as a perfect transitional form between two major kinds of animals—reptiles and birds.

4) The "Maxberg" specimen (Fig. 4) found in 1956 close to the site of the London specimen.

5) The Teyler specimen (Fig. 5), originally found in 1855, six years before the single feather and the London specimen, but misidentified until 1970 as a pterosaur or flying reptile. It has resided in the Teyler Museum of Haarlem, Netherlands for nearly 130 years.

6) The Eichstätt specimen (Fig. 6) originally found in 1951

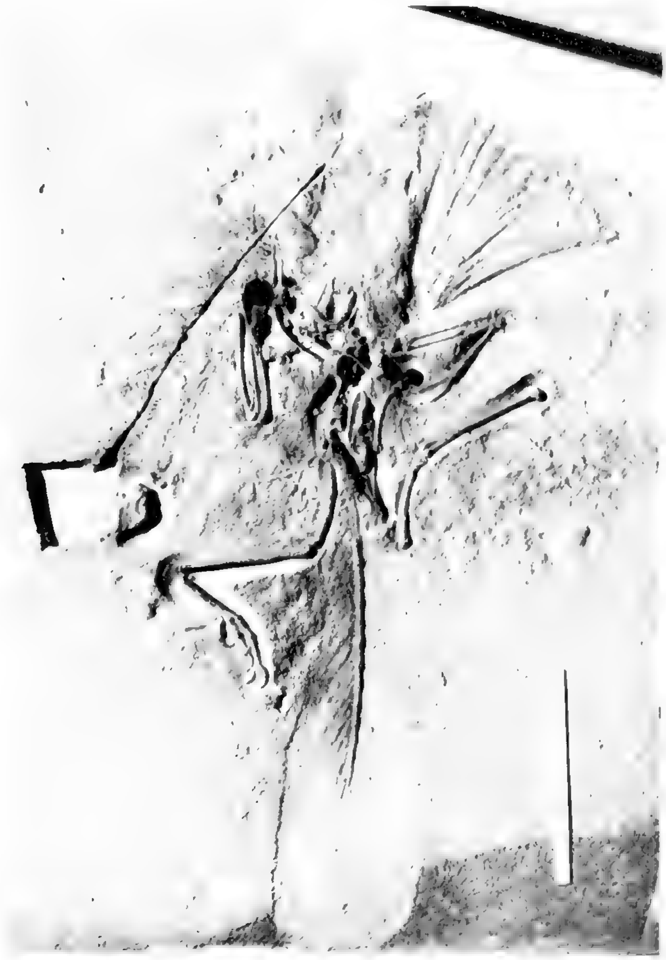

FIGURE 2. The London specimen of *Archaeopteryx* to which Hermann von Meyer first applied the name *Archaeopteryx lithographica* in 1861. Now it is displayed in the British Museum (Nat. Hist.) in London. (From Ostrom 1976*b*.)

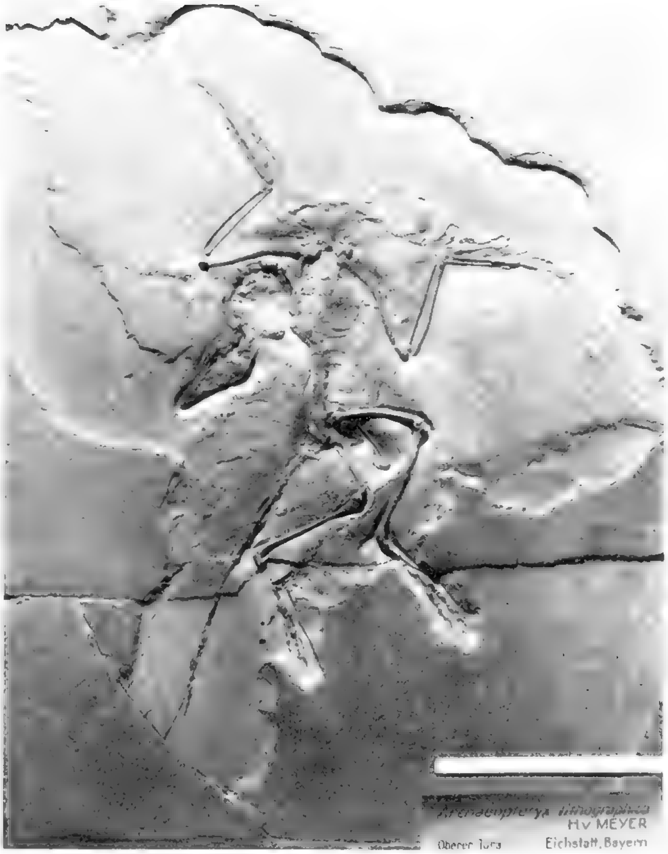

FIGURE 3. The famed Berlin specimen of *Archaeopteryx* discovered near Eichstätt, West Germany in 1877. It is the prized possession of the Humboldt Museum of East Berlin. (From Ostrom 1976*b*.)

and misidentified as the small carnivorous dinosaur *Compsognathus,* until it was correctly identified in 1973 (Mayr 1973). It now resides in the Jura Museum in Eichstätt, West Germany.

It is clear from several of these specimens that *Archaeopteryx* had well-developed contour, or vaned, feathers. In fact, these appear to have been essentially like modern vaned feathers with barbs, barbules, and probably microscopic hooklets on the barbules—as is indicated by the parallel arrangement of the barbs in Figure 1, the impression of the feather referred to *Archaeopteryx*. From this evidence there can be no doubt that *Archaeopteryx* was a true bird. But if there could be any question, a single skeletal feature of *Archaeopteryx* appears to confirm that identification. That is the presence of a furcula or wish-bone preserved in the London and "Maxberg" specimens—a bone that until recently was believed to be unique to birds and an integral skeletal component of their flight apparatus. That element may have special phylogenetic significance because Barsbold (1983) has reported very similar symmetrical mid-line pectoral elements in a few Asiatic theropod dinosaurs, the reptilian group that some (Ostrom 1975, 1976*b*) believe to include the ancestry of birds (see Gauthier, this volume). If Barsbold's bone can be shown to be homologous to the avian furcula, that would be strong evidence in support of a theropod-avian relationship. But it raises some interesting questions that bear on the beginnings of flight. In birds, this element is an important component of the skeletal flight apparatus, acting as an attachment site for flight muscles and perhaps serving as a "brace" between the shoulders. What role a furcula might have played in a flightless bipedal theropod dinosaur is not known. That raises the intriguing thought that perhaps the furcula in *Archaeopteryx* had some nonflight function as well! That would be consistent with the weak coracoid and acrocoracoid, and the missing sternum and triosseal canal.

Of special interest in this controversy over the way in which bird flight might have arisen is the arrangement of the enlarged feathers on the forelimbs of *Archaeopteryx*, best illustrated in the Berlin specimen (Fig. 3). There can be no doubt that these feathers had asymmetrical vanes, as pointed out by Feduccia and Tordoff (1979), and were arranged in a winglike configuration (Savile 1957), all of which surely suggests that this animal could have flown. Perhaps. Some researchers have argued for varying degrees of flight capability in *Archaeopteryx* on the basis of diverse evidence and interpretation: Yalden (1970, 1971), Heptonstall (1970, 1971), Bramwell (1971), and Olson and Feduccia (1979). The evidence is complex and perhaps even contradictory, but if *Archaeopteryx* did fly, I personally doubt that it could have flown very well, because it lacked a number of critical skeletal features that are present in modern flying birds.

FIGURE 4. The "Maxberg" specimen of *Archaeopteryx* found in 1956 in the same Solnhofen quarry area that produced the London specimen nearly a century earlier. This is the only specimen that is privately owned. (From Ostrom 1976*b*.)

FIGURE 5. The Teyler or Haarlem specimen of *Archaeopteryx* originally discovered in 1855. Misidentified as a pterosaur until 1970, it is now on display in the Teyler Museum of Haarlem, Netherlands. (From Ostrom 1976*b*.)

First of all, there is no sign of a sternum or breastbone in any of the specimens of *Archaeopteryx* (Fig. 7), contrary to Marsh's (1881) or de Beer's (1954) conclusions. Second, the coracoid bone of the shoulder skeleton is not strutlike, and therefore did not have an ossified connection to the sternum. Third, the fingers and metacarpals are not fused together. Finally, there is no triosseal canal resulting from a prominent acrocoracoid process, because that process was not sufficiently developed (see Ostrom 1976*a*). The significance of these deficiencies is not trivial in a presumed flying bird: allow me to explain.

The sternum (Fig. 7) is the major attachment site of the flight muscles, although the furcula also is involved. Does its absence in *Archaeopteryx* mean weak flight muscles? In modern flying birds the coracoid is a robust bony brace between the shoulder socket and the sternum, which resists depression of the shoulder socket and thereby conserves all flight muscle contractile forces to power the flight stroke of the wings (Fig. 7, 8). In *Archaeopteryx* the coracoid was only a thin sheet of bone and could hardly have functioned as a strong strut (Fig. 9). In *Archaeopteryx* the fingers and metacarpals were free and did not form a robust skeletal platform for firm anchorage of the primary flight feathers (Fig. 10, 11). An important and curious muscle in avian flight machinery is the supracoracoideus, which, although attached to the ventrally placed sternum, actually elevates the wing, and so adds power to the recovery stroke (see Fig. 7, 8). That arrangement is possible because of the triosseal canal–acrocoracoid complex, which functions as a pulley and thereby reverses the action of the supracoracoideus muscle. The absence of the triosseal canal in *Archaeopteryx* (Ostrom 1976*a*) means that the supracoracoideus muscle could not possibly have functioned to power the recovery stroke of the wing as it does in modern birds (Fig. 7, 8). In short, these features of *Archaeopteryx* do not preclude powered flight, but they certainly do indicate a primitive state of anatomical development that suggests a very poor flight capability in this earliest bird.[1]

Now, having said that, what do these specimens of *Archaeopteryx* indicate about cursorial versus arboreal habits? Was *Archaeopteryx* a ground-dwelling predator? Or did it launch itself from the trees on an awkward flapping glide? First of all, the

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[1] In anticipation of critics who will note that bats fly remarkably well without a sternal keel and without a triosseal canal or a recovery stroke powered by a reversed M. supracoracoideus, let me emphasize the following: a) Bat flight evolved from a very different ancestral stock, almost certainly quadrupedal and definitely mammalian—not reptilian. b) Bat flight arose via a completely different sequence of events and conditions. c) Flight in bats is powered by the M. pectoralis (which meet in a midline raphe—a connective tissue septum analogous to the bony sternal keel of carinate birds, but of less mass) and M. subscapularis. d) The wing recovery stroke is powered in part by several parts of the dorsally situated deltoideus and suprascapular muscles, facilitated by a highly mobile scapular blade and shoulder skeleton (in sharp contrast to the immobile shoulder skeleton of birds). In short, bat and bird flight mechanics are very different (see Vaughan 1970) and arose by very different pathways.

FIGURE 6. The Eichstätt specimen of *Archaeopteryx* preserving superb skeletal details, but lacking distinct impressions of feathers. (From Ostrom 1976*b*.)

hindlimbs are strongly developed and long, with a long tibia plus metatarsal length relative to femur length—slightly more than 2 to 1 (for example, see Fig. 3). That is consistent with a cursorial habit, but it does not preclude an arboreal mode of life.

The reversed hallux of *Archaeopteryx* (Fig. 12) is not especially elongated, as it is in most perching and predatory birds. Also, it is positioned rather high on the metatarsus in contrast to a very low position in perching birds. Could this hallux have effectively grasped a branch? The most compelling evidence that argues for a cursorial ground-dwelling mode of life for *Archaeopteryx* is the form and size of the unguals of the toes. In perching birds and birds of prey, the unguals are strongly curved and sharp, they possess prominent flexor tubercles to which the flexor muscles attach, and—most important—the ungual of the hallux is much longer than that of the other toes. In Figure 13 you see a comparison of the unguals of the first toe (hallux) and the middle or third toe of several kinds of birds. In *Archaeopteryx,* all unguals are less strongly curved and not especially sharp, the flexor tubercles are subdued and far less developed, and finally, the hallux ungual is significantly shorter than those of the other toes when compared to perching or predatory birds of today (Ostrom 1974). In these ways, the unguals of *Archaeopteryx* closely resemble the unguals of living ground birds like pheasants, chickens, partridges, etc.

My conclusion: *Archaeopteryx* appears not to have had a foot designed for perching or grasping—which suggests that it was probably not a frequent occupant of trees. Let me emphasize at this point that I am not saying that *Archaeopteryx* could not have been arboreal, but rather that I see no evidence that sug-

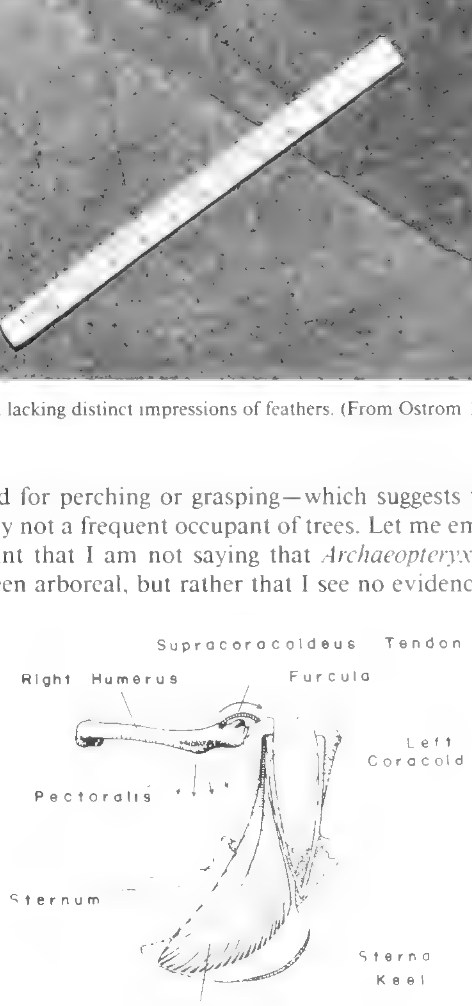

FIGURE 7. Anterolateral view of the shoulder skeleton and sternum of the modern pigeon (*Columba livia*) to show the general relationships of the skeletal-muscular systems. The flight muscle (M. pectoralis) has been removed (ventrally directed arrows show pectoralis action) to reveal the underlying M. supracoracoideus. The latter powers the recovery stroke of the wing because of the pulley-like action imparted to it (upper curved arrow) by the triosseal canal formed by the junction of the scapula and the acrocoracoid process of the coracoid. See Figure 8. (Redrawn from George and Berger 1966.)

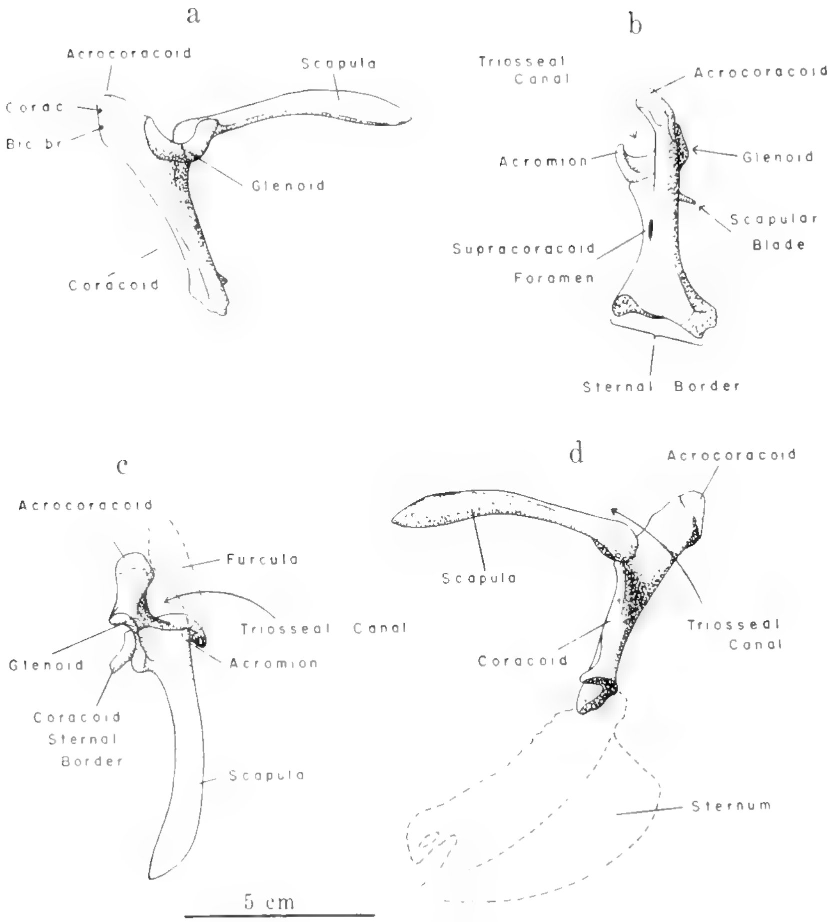

FIGURE 8. Four views of the left scapulocoracoid of the turkey vulture *Cathartes aura* show the architecture of the triosseal canal. That structure is absent in *Archaeopteryx*, as Figure 9 shows. It is this special shoulder feature that reverses the action of the ventrally placed M. supracoracoideus so that it acts as a wing elevator rather than a wing depressor. (a) lateral aspect, (b) anterior aspect, (c) dorsal view, (d) medial view. Abbreviations: Bic. br. = the site of origin of the M. biceps brachii; Corac. = the site of origin of the M. coracobrachialis anterior. (From Ostrom 1976*a*.)

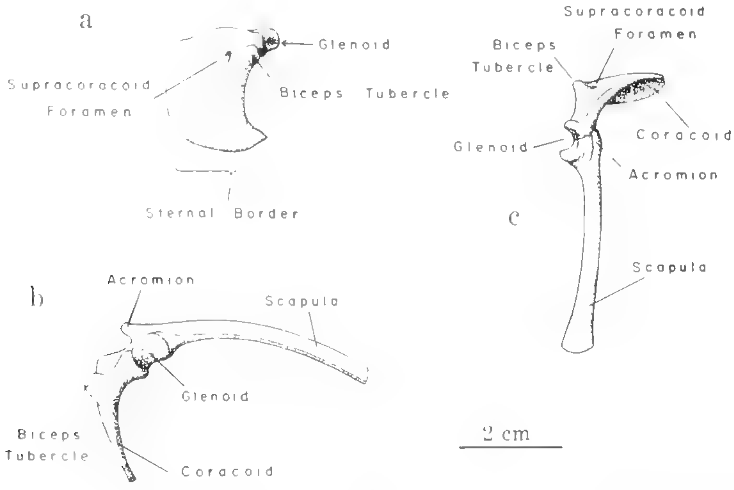

FIGURE 9. Three views of the shoulder skeleton of *Archaeopteryx* as reconstructed by the author from the London, Berlin, and "Maxberg" specimens. (a) anterior view, (b) lateral view, (c) dorsal view. Notice that the absence of a pronounced acrocoracoid process of the coracoid results in the absence of the triosseal canal which means that the M. supracoracoideus of *Archaeopteryx* must have acted as a wing depressor rather than powering the recovery stroke of the wing. (From Ostrom 1976*a*.)

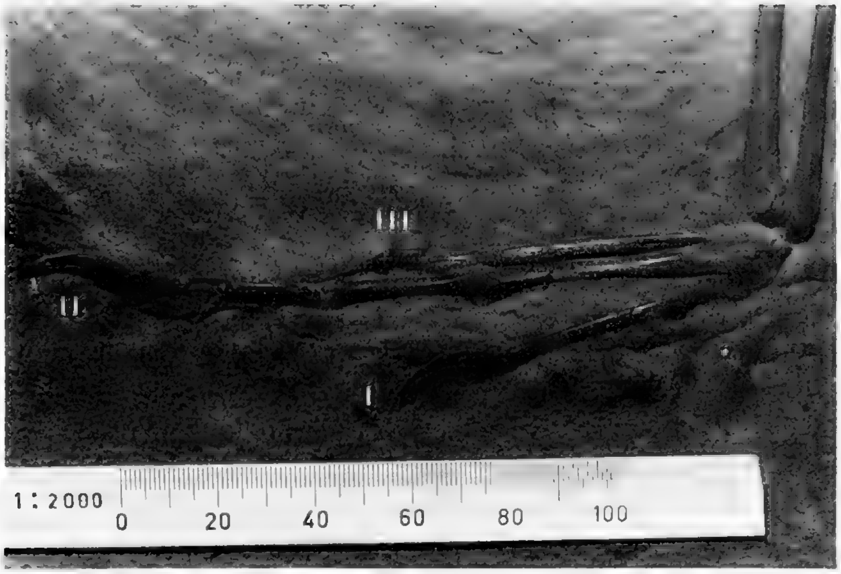

FIGURE 10. The right manus and carpus of the Berlin specimen of *Archaeopteryx* seen in dorsal aspect. Notice the separated fingers and unfused metacarpus. Contrast this with the construction of the modern avian carpometacarpus and manus of Figure 11. Scale divisions = 0.5 mm.

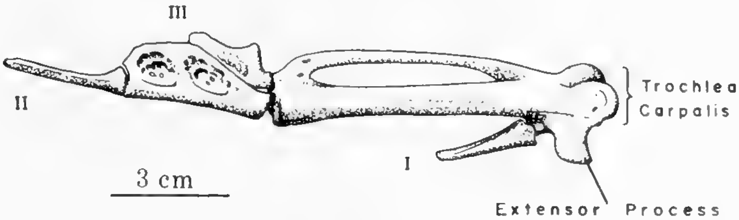

FIGURE 11. The right manus and carpo-metacarpus of the turkey vulture *Cathartes aura* in dorsal view for comparison with Figure 10. There is some debate about the digit identification in *Archaeopteryx* and modern birds, but that is not an important issue here. (From Ostrom 1976*a*.)

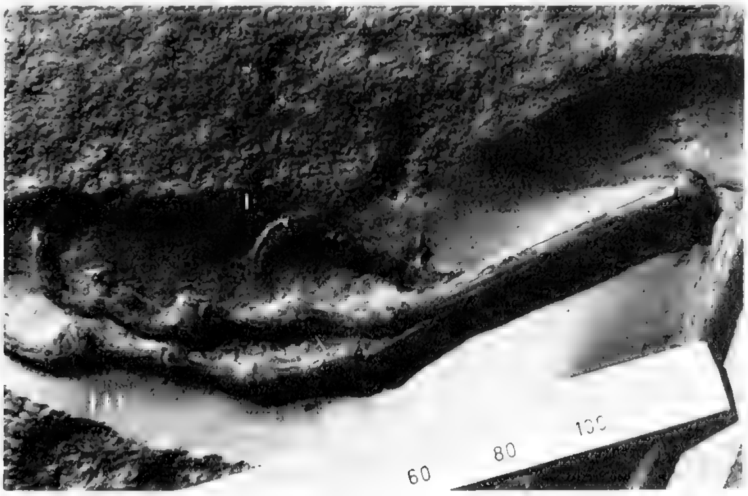

FIGURE 12. The left pes and metatarsus of *Archaeopteryx* (London specimen) in lateral view. Notice the elevated position of the hallux (I) articulation with the metatarsus. Scale divisions = 0.5 mm. (From Ostrom 1976*b*.)

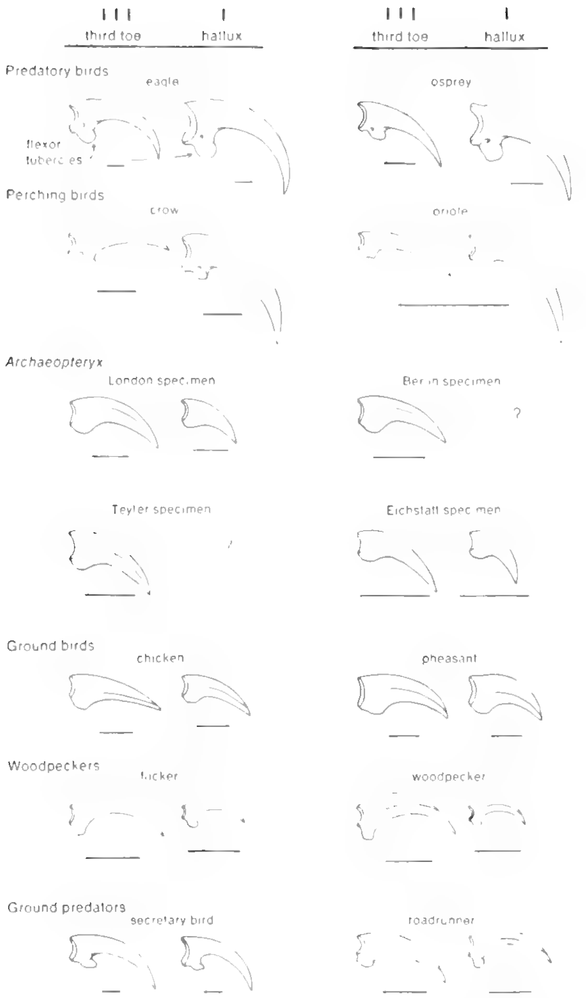

FIGURE 13. Ungual phalanges (without the horny claws) from the feet of selected bird types compared with those of four specimens of *Archaeopteryx*. Each example includes the ungual of the middle anterior toe (III) on the left (columns 1 and 3) and the hallux ungual (I) on the right (columns 2 and 4). All digit III unguals (columns 1 and 3) are drawn to unit length for convenient comparison and each companion sketch of digit I unguals (columns 2 and 4) is drawn to the same scale. Scales are indicated by the horizontal lines, all of which equal 5.0 mm. Orientations are standardized with the articular facets drawn in the vertical position. In nearly all respects, the unguals of *Archaeopteryx* resemble those of ground-dwelling birds more closely than all others, featuring slight curvature; robust construction; and shallow, poorly defined flexor tubercles. Notice that in all (except the ground birds) the flexor tubercle is very prominent and sharply defined. Also, the hallux ungual is longer than the other unguals in most passerines (and many predatory birds). In addition to the four specimens of *Archaeopteryx*, the examples sketched include: the bald eagle *Haliaeetus leucocephalus* and the fish hawk or osprey *Pandion haliaëtus*, the crow *Corvus brachyrhynchos* and the oriole *Icterus spurius*, the chicken *Gallus gallus* and the pheasant *Phasianus colchicus*, the flicker *Colaptes cafer* and the woodpecker *Picus viridis*, the secretary bird *Sagittarius serpentarius* and the roadrunner *Geococcyx californianus*. (From Ostrom 1974.)

gests an arboreal habit. Instead, I see clear indications of a ground-dwelling animal.

DISCUSSION

These facts present us with a dilemma. The anatomy of *Archaeopteryx* suggests a very poor *powered*-flight capability, if any. That has led to a general consensus that *Archaeopteryx* was

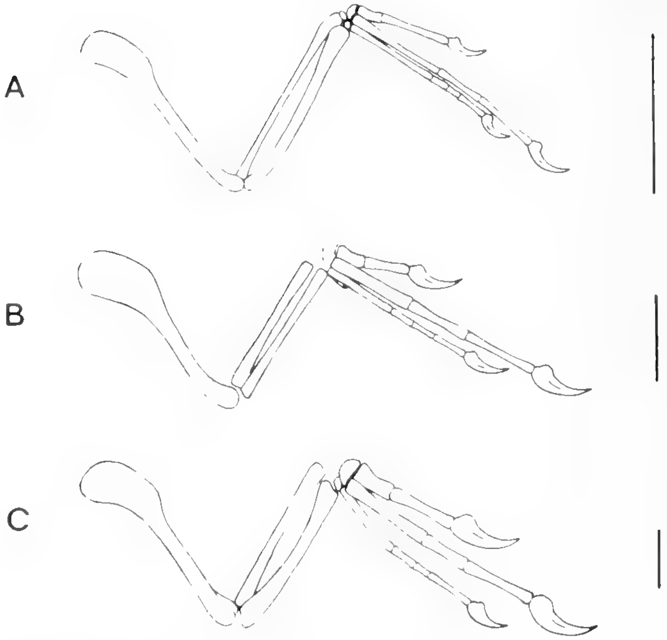

FIGURE 14. Outline drawings of the right forelimb of *Archaeopteryx* (A) compared with those of theropods *Ornitholestes* (B) and *Deinonychus* (C) to demonstrate the remarkable similarity in hand configuration and proportions. The humeri are drawn to the same length to facilitate comparison and reduce size-related differences. Relative sizes are indicated by the vertical lines, all of which equal 5.0 cm. (From Ostrom 1975.)

at least a glider, which leads to the seemingly logical conclusion that *Archaeopteryx* must have been arboreal. The only other alternative is that it launched itself half gliding, half flapping from the ground up—perhaps off sea cliffs. The last point could be true, but the Solnhofen Limestones, from which all of the specimens of *Archaeopteryx* were recovered, contain almost no detrital sediments; this fact suggests that nearby terrestrial relief was low and that any high cliffs would have been many miles away from the Solnhofen lagoons.

The evidence of the specimens of *Archaeopteryx* clearly suggests some degree of flight—no matter how feeble—at that early stage, but powerful, flapping flight seems most unlikely. Those same specimens, however, suggest that *Archaeopteryx* was not arboreal, so a gliding entry into avian flight is equally doubtful. (Some researchers maintain, on aerodynamic grounds, that true gliding flight could not have led to flapping flight [Savile 1962]; see Padian 1982, 1983, for a recent review of this theory.) In fact, there is no evidence—and I underline the word *evidence*—that bird flight began from the trees down. What evidence there is all points to a highly adapted bipedal cursor and a "ground-up" origin of flight.

Some years ago, because I was intrigued with the seemingly paradoxical evidence preserved in the specimens of *Archaeopteryx*, I suggested that avian flight began in a fast-running, bipedal, ground-dwelling predator (Ostrom 1974, 1979). The idea was not new, except for the predator part. Because of the striking anatomical similarities between *Archaeopteryx* and contemporaneous small carnivorous dinosaurs (Ostrom 1975, 1976*b*), I suggested that the "protowing," with its dinosaurlike skeletal anatomy, was first a predaceous appendage bearing "proto-

feathers" that increased the forearm surface area—not for flight, but rather to enhance its prey-catching properties (Fig. 14). At the time, I was well aware that this was a far-fetched idea, but the skeletal anatomy of the forelimb seemed convincing, and there could be no doubt that *Archaeopteryx* and its ancestors were both obligate bipeds and predators, most probably preying on insects. My objective then and now is to revive the debate, or controversy: Did bird flight begin in the trees or from the ground? The arboreal theory that has prevailed for more than half a century intrinsically seems more logical than the "bootstrap" cursorial theory. But on the other hand, the actual physical evidence (as opposed to any hypothetical historical scenario) points very strongly toward a cursorial origin of avian flight.

That hypothesis has been reinforced by Russell Balda and his associates at Northern Arizona University in an imaginative paper (1983) entitled "The Physics of Leaping Animals and the Evolution of Preflight." Space does not permit a full explanation of their hypothesis, but in brief, they propose that avian flight began with a bipedal cursorial ancestor that used its arms to help maintain balance and active control of body attitude while running and leaping. They point out that control of changes in body attitude (roll, pitch, and yaw) is paramount for any animal that becomes airborne—even if such aerial excursions are just simple leaps. Such control could be imparted by the forelimbs, where angular momentum and moments of inertia of the limbs provide the controlling forces (as in a broad jumper, for example), or by the aerodynamic properties of incipient wings in a leaping "proavis." Balda and his colleagues note that a jumping animal's center of mass will follow a ballistic trajectory that cannot be changed while airborne unless it can provide lift or thrust—in other words, aerodynamic deflection of the animal's moment of inertia that was imparted at the instant of leaping. The angular momentum and moments of inertia of the limbs (and tail) can alter orientation of the body in flight, as in the case of a spring board diver, but without lift or thrust, the (diver's) trajectory is predetermined at the moment of liftoff. By enhancing the extremities into incipient aerodynamic surfaces (as well as appendages with moments of inertia), both body attitude and flight trajectory can be changed. In short, the flight apparatus of birds could have begun as a stabilizing or control mechanism in a ground-dwelling biped. Without such controls, powered avian flight probably could not have evolved.

Of course, control of body attitude is just as critical for the airborne hypothetical arboreal "proavis" that launched itself from the tree tops, but in the presence of strong evidence for a cursorial, rather than an arboreal adaptation in *Archaeopteryx*, I am a firm believer in the cursorial origin of bird flight.

Conclusions

Unfortunately, we can never know how the different forms of animal flight began. Nevertheless, it was a significant evolutionary event—not once, but many times. It would seem that most nonavian forms of flight probably began from elevated perches. But the beginning of flight in birds may have been different. The most important clue in support of that may be the sophisticated and unique bipedal design of birds.

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Mechanical Constraints on the Evolution of Flight

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Introduction

Probably more than half the species of animals alive today can fly at some stage of their life cycles. Flying animals are found in such profusion that it is easy to believe that there are no limits to the types that can evolve. Actually, the body forms available for flying animals are confined within certain boundaries, which are set by mechanical factors. Body mass, in particular, is one of the most important (and least discussed) characters determining whether a nonflying animal has any chance of evolving the power of flight. The mass of a potential flying ancestor has to be within a comparatively narrow "window." Specialization of an animal that can already fly opens up a somewhat wider, though still limited, range of mass. The mechanical basis for limits to the body mass of flying animals has been explained by Pennycuick (1975*b*). Two of the factors involved, power margin and frequency scope, will be summarized here, as background for discussing the origin of flight.

Power Required to Fly

The term "flight" may mean anything from the extremely strenuous maneuvers of hummingbirds to the soaring flight of vultures. The amount of power required from the muscles varies over a wide range, depending on the size of the animal and on what exactly it is doing. If we confine our attention initially to steady horizontal flight in some particular animal, then the power required varies with the speed, in some such way as illustrated in Figure 1. Flight at very low speeds, or zero speed (hovering) is invariably more strenuous than flight at a moderate forward speed. The curve of power versus speed initially declines, then reaches a minimum, then increases again at high speeds. Two points on this curve are especially significant. First, there is a definite "minimum power speed," at which flight is less strenuous than at either faster or slower speeds. Second, there is a somewhat higher "maximum range speed" at which the ratio of speed to power reaches a maximum. This is the speed at which the animal has to fly if it is to maximize the distance flown per unit of fuel consumed.

Power Margin and Body Mass

The term "power margin" is defined here as the logarithm (to base 10) of the ratio of the power available from the muscles to that required to fly horizontally at the minimum power speed. Thus an animal with a power margin of zero can muster exactly the amount of power needed to fly at its minimum power speed, but cannot maintain height at either faster or slower speeds. A power margin of +1 means that 10 times as much power is available as is required, and −1 means that only one-tenth of the requirement can be met. Power margin in this sense is very strongly dependent on the size or mass of the animal. In essence the argument is in two parts as follows:

1. The power required to fly at the minimum power speed can be represented as the product of the drag times the speed. The drag is proportional to the mass in geometrically similar animals, whereas the minimum power speed increases in proportion to the one-sixth power of the mass. Therefore the power required varies with the seven-sixths power of the mass. That is, a double-logarithmic plot of the power required versus the mass would yield a straight line, with a slope of seven-sixths, as shown in Figure 2.

2. The power available from the muscles is the work done in each contraction times the flapping frequency. The work done is proportional to the muscle mass, and hence to the body mass, whereas the flapping frequency is lower in larger animals. In the case of maximum exertion, contraction frequency is proportional to the minus one-third power of the mass (Hill 1950). The maximum power available is therefore proportional to the two-thirds power of the mass.

Figure 2 shows two lines for power available, both with the same slope (two-thirds). The higher one represents vertebrate muscle, and the lower one is for insect asynchronous muscle. The latter produces less power at any particular body mass (or frequency) than vertebrate muscle, for reasons explained by Pennycuick and Rezende (1984). The solid straight lines refer to anaerobic muscle, capable only of intermittent activity. The dotted lines are for aerobic muscle, used for sustained cruising locomotion. These produce less power for a given muscle mass, because the contractile machinery is diluted with noncontractile mitochondria. The difference between aerobic and anaerobic

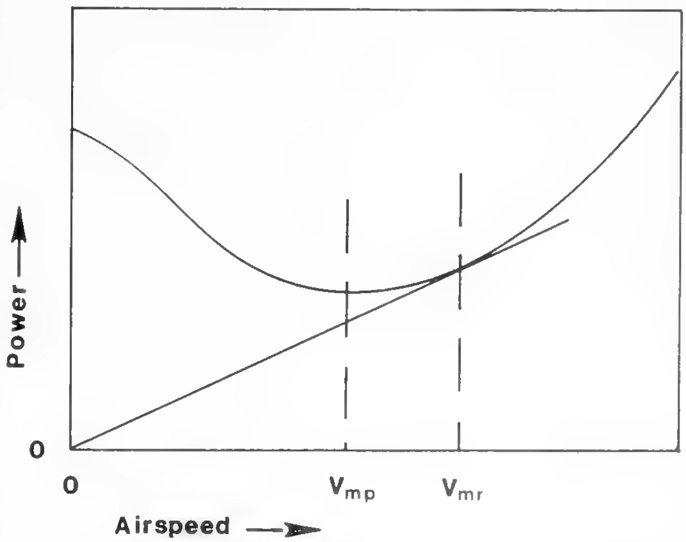

FIGURE 1. The power required to fly (rate of energy expenditure) in steady horizontal flight varies with the forward speed. V_{mp} is the "minimum-power speed." V_{mr} is the "maximum-range speed," at which the ratio of speed to power (and hence of distance travelled to energy consumed) is a maximum. It can be found by drawing a tangent to the curve passing through the origin, as shown

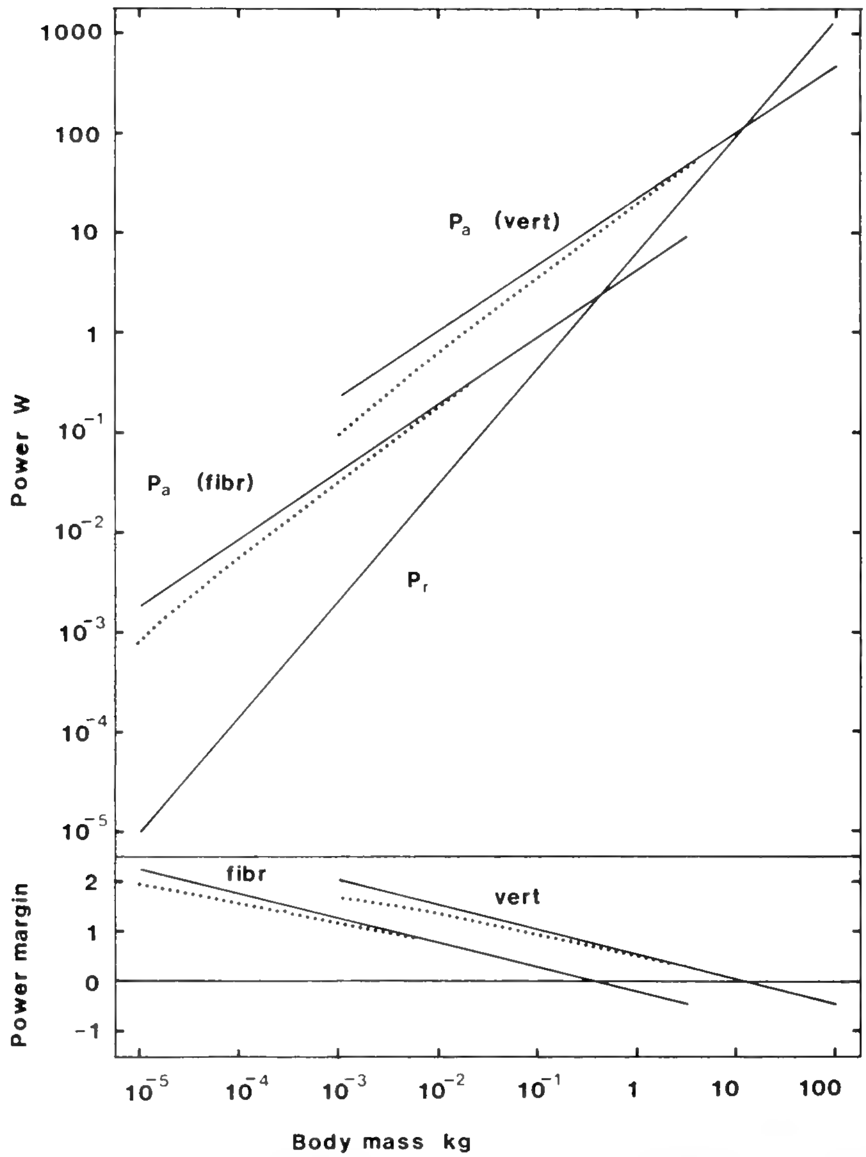

FIGURE 2 P_r, the power required to fly at the minimum power speed, is shown as increasing with the seven-sixths power of the body mass. This is an oversimplification, but the general trend should be approximately as shown. Two straight lines are shown for P_a, the power available from anaerobic flight muscles: one for vertebrate and the other for insect asynchronous (fibrillar) muscles. The dotted lines are power available from aerobic muscles. Below, power margin, as defined in the text, is shown for insect asynchronous and vertebrate fliers.

muscle becomes more pronounced as mass decreases, and contraction frequency increases. Eventually, at very small sizes, the aerobic power-available line bends around until its slope is one, rather than two-thirds.

The vertical distance between the converging lines of Figure 2 represents the power margin, as defined above. The vertebrate lines have been plotted on the assumption that a 12 kg bird (like a condor) has a power margin of zero and requires about 115 W of mechanical power to fly at its minimum power speed. On this basis, the lines diverge to the left, giving a power margin of 0.55 at a body mass of 1 kg, 1.01 at 0.1 kg, and 1.55 at 0.01 kg. Thus, it is easy to muster enough power to fly horizontally if the animal's body mass is 100 g or below, less easy at 1 kg, and progressively more difficult above that. Power margin is plotted in a separate graph at the bottom of Figure 2.

Upper Limit of Mass

The power margin argument should not be interpreted to imply that there is a sudden boundary, beyond which "flight" is impossible. There are many forms of flight, some of which require more power than others. As body mass is progressively increased, the most strenuous forms of flight become impossible, in order of their demand for power. First, the ability to hover continuously is lost. Only hummingbirds can do this, although transient hovering is possible in somewhat larger birds. The

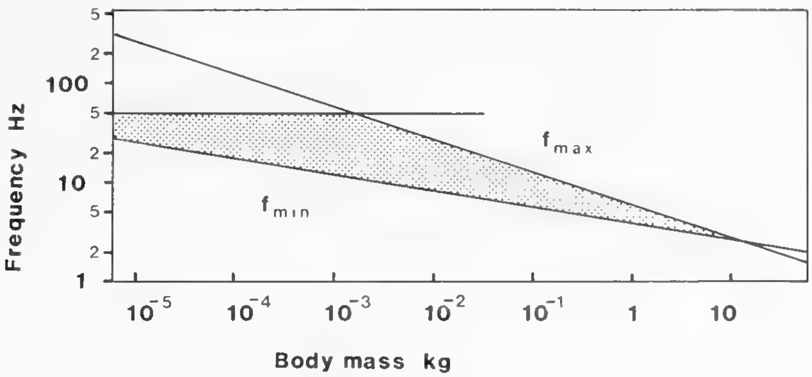

FIGURE 3. Minimum and maximum wingbeat frequencies converge as mass increases. The stippled region is available to vertebrate fliers. The horizontal upper boundary, which is approximate, reflects the minimum time taken to reset the muscle after each contraction. This upper boundary does not apply to insects with asynchronous flight muscles.

next most strenuous form of flight is jump takeoff on an upward trajectory. Birds up to about 2 kg can do this, after which a takeoff run becomes necessary, or the problem is avoided by downward takeoff from an elevated perch. Horizontal flight at the maximum range speed seems to be possible up to about the same limit. Very large birds cannot attain the appropriate speed for economical cruising, so that they are obliged to fly at a lower, less efficient speed. Finally, horizontal flight at the minimum power speed is known to be possible, at least intermittently, in birds up to about 12 kg. It does not follow that bigger birds cannot fly, only that they cannot fly horizontally. Large birds typically spend most of their time gliding. They get the energy for flight from movements of the atmosphere rather than from their own muscles. This is called soaring. A bird that did not need to take off from a horizontal surface might well be able to make do with only enough muscle power to allow powered flight at a shallow downward angle. Flying animals larger than the largest living species might be possible if the requirement for horizontal flight were relaxed.

Frequency Scope

Another factor that sets both upper and lower limits to the mass of flying vertebrates (though not a lower limit for insects) is the frequency at which the wings are flapped. Any particular flying animal has to select its wingbeat frequency from within a certain range, whose upper and lower limits are set by different factors. The upper limit is determined by the strength of the bones and muscle attachments. Hill (1950) argued that the maximum frequency at which any limb can be driven varies with the minus one-third power of the body mass in geometrically similar animals. This line is plotted in Figure 3 and is the basis of the variation in power available from the muscles, discussed above. The lower limit is based on the need to provide sufficient relative airflow over the wings to supply lift and propulsion. It has been argued by Pennycuick (1975*b*) that this lower limit should vary with the minus one-sixth power of the mass. This line is also plotted in Figure 3. This diagram, as before, refers to geometrically similar animals. The minimum and maximum wing-beat frequencies converge as mass increases, until at some body mass (here assumed to be 12 kg) the bird is only just able to fly when flapping at its maximum frequency. Smaller animals have a progressively wider range of wingbeat frequencies available, while bigger ones cannot beat their wings fast enough to fly horizontally.

Lower Mass Limits

At the lower end of the vertebrate size range, animals with body masses in the region of 1 g reach an upper limit for the maximum wingbeat frequency. This is because synchronous muscles (in which the electrical activity is synchronized with the contractions) require a minimum time to complete a cycle of contraction and relaxation, and this in turn limits the maximum frequency of contraction. Recently Josephson and Young (1985) have discovered a muscle in the tymbal organ of a cicada that can contract synchronously at 550 Hz, but this muscle is only required to deliver a small amount of power. The upper limit seems to be around 100 Hz for synchronous flight muscles. An animal whose maximum frequency is limited in this way is no longer able to develop the maximum power which the strength of its parts would otherwise allow, and so becomes restricted in the range of "sprint" maneuvers available to it.

This lower mass limit applies to vertebrates, and to those insects which have synchronous flight muscles. Higher insects have developed asynchronous ("fibrillar") muscles, which can deliver enough power for flight at much higher frequencies than the synchronous type, and are thus suitable for smaller animals. Insect asynchronous flight muscles can attain contraction frequencies exceeding 1 kHz, and are believed to be limited ultimately by properties of the contractile mechanism, which place an upper limit on the strain rate (Weis-Fogh and Alexander 1977). The active strain in insect asynchronous muscles is an order of magnitude less than in vertebrate flight muscles. This leads to a correspondingly lower specific power output at any given contraction frequency, and also requires the muscle action to be magnified by a suitable lever system, as seen in the indirect flight muscle systems of higher insects. Even if vertebrates were to develop asynchronous muscle, the evolution of gnat-sized forms would be difficult, because the vertebrate skeleton could not readily be adapted to produce a sufficient amplitude of wing movement from such a small amount of muscular shortening. Asynchronous muscles are not suitable for larger animals. At any particular body mass, an animal with asynchronous muscles

has a lower power margin than one with synchronous muscles, as shown in Figure 2. Insects that fly with asynchronous muscles attain a maximum body mass of about 40 g, and could theoretically go to about 200 g before reaching a power margin of zero. Such an insect would be the asynchronous equivalent of a condor, barely able to maintain horizontal flight.

Body Mass and Potential Diversity

Lack of Diversity in Large Flying Animals

If a flying animal is under pressure to evolve large body size for any reason, it can do so only at the expense of narrowing the available choice of shape and size for its wings. Very large representatives (over 8 kg) of such groups as storks, cranes, vultures (Old and New World), and pelicans all converge on a standard wing shape, with broad tips, emarginated primaries, and aspect ratios around 7–10. This "standard" wing for large birds seems to be long enough for acceptable efficiency in horizontal flight, while being short enough to allow an adequate flapping frequency at takeoff. Variation in favor of one requirement incurs a penalty in the other. For instance large bustards have somewhat shorter wings than other large birds, which seems to facilitate takeoff but restricts their powers of sustained flight. Large albatrosses have much longer wings than other large birds, but have only been able to achieve this at the expense of relaxing takeoff requirements, in that they only need to take off from water or sloping ground.

It would seem that as a body mass of about 10 kg is approached, and passed, the "potential diversity" of flying animals becomes progressively more limited. Only a few kinds of flying animals seem to be possible at this level of mass. At still larger sizes, such as have been claimed for the fossil teratorn *Argentavis* and the Cretaceous pterosaur *Pteranodon,* horizontal flight would be impossible for the reasons illustrated by Figures 2 and 3. Such sizes are only accessible to highly specialized animals that can do without horizontal flight, perhaps as a result of specially favorable (and temporary) environmental conditions. Going downwards in mass from 10 kg, power margin rapidly increases in animals with wings of normal shape. At lower masses, a positive power margin can still be maintained with wings of unusual shape or size. For example, below about 1 kg, flight is possible in birds with wings of such reduced size that they can be used in water as well as in air (Alcidae). Below 100 g, a tremendous variety of wing shapes and sizes is possible, without compromising the power of flight. This potential diversity extends down to the 10 g level, then dwindles again to zero (in vertebrates) at the 1 g level, for the reasons given above.

In today's highly evolved bird and bat fauna, we may take it that the actual diversity of living species is a fair reflection of the potential diversity. Clearly the present diversity is greatest in the range of mass from 10 g–1 kg, and dwindles sharply above and below those limits. If the number of living species of birds and bats could be plotted against mass, probably there would be many more in the range 10–100 g than between 100 g and 1 kg. In the days before flying animals evolved, the actual diversity of species did not yet exist, but the potential diversity already did. A nonflying animal, destined to evolve the power of flight, will have some structures that are not yet wings, and do not, initially, perform well as such. To have a chance of developing flight, it must be in a region of high potential diversity for flying animals. A nonflying animal over 1 kg is very unlikely to evolve flight, because only a limited range of specialized animals can fly successfully at such large sizes. To have the best chance of success, the ancestor should be in the mass range 10–100 g, where oscillating maladapted limbs at inappropriate frequencies can still produce acceptable results.

Arboreal Versus Cursorial Origin

Evidently a nonflying animal's mass is one of its most important characteristics in relation to its potential as an ancestor for flying animals. Modern arboreal animals abound in the required mass range of 10–100 g, but cursorial animals are much larger, for reasons connected with the mechanics of running. Field observations of undisturbed wild cursorial animals in cruising locomotion (Pennycuick 1975*a*) show that for a particular gait, such as quadrupedal trot or canter, or bipedal run, each species chooses cruising speeds within a restricted range. Corresponding speeds are higher in larger animals, about in proportion to the square root of the linear dimensions, in agreement with the dynamic similarity argument of Alexander and Jayes (1983). Selection pressure for fast cruising locomotion, imposed by the ecological requirements of foraging, results in a tendency towards large size (Pennycuick 1979). Typical cursorial animals capable of sustained running, such as antelopes, dogs, hyenas, kangaroos, and ratites have body masses ranging from about 5 kg up to a few tonnes. Dinosaurs also were characteristically medium-sized to very large animals, with few mouse-sized representatives. A cursorial, bipedal archosaur ancestor would more probably have been in the size range of ostriches and moas than in that of *Archaeopteryx.* Such large animals could not have evolved flight directly. The line must have passed through a phase of smaller forms, which was most probably achieved in the ancestors of birds and pterosaurs by first changing from cursorial to arboreal locomotion (below).

Gliding Route to Powered Flight

Relationship of Gliding to Powered Flight

Living animals exhibit many levels of flying ability, some of which can be seen as possible stepping stones in the development of powered flight. The term "gliding" covers any form of flight in which no power is supplied from the animal's muscles. It includes some of the most elementary forms of flight, as in parachuting plant propagules, and also some of the most elaborate, as in soaring birds. There is no sharp boundary between parachuting and gliding. Rather, there is a spectrum, definable in terms of gliding angle, ranging from vertically downwards in pure parachuting to an estimated 1:23 for the wandering albatross (*Diomedea exulans*) (Fig. 4).

Sustained, horizontal gliding flight is not possible. To fly horizontally, some power must be supplied by the animal's muscles. The flatter the gliding angle, the less power is required to bring the flight path to the horizontal. To develop powered flight in an animal that can already glide at a reasonably flat angle, further adaptations are required that develop a small amount of forward thrust, which in turn requires some muscle power to be supplied. The easiest entry point is to exert thrust while gliding at the minimum power speed (Fig. 1), since the power required is least for an animal that can already glide at that speed. It is much

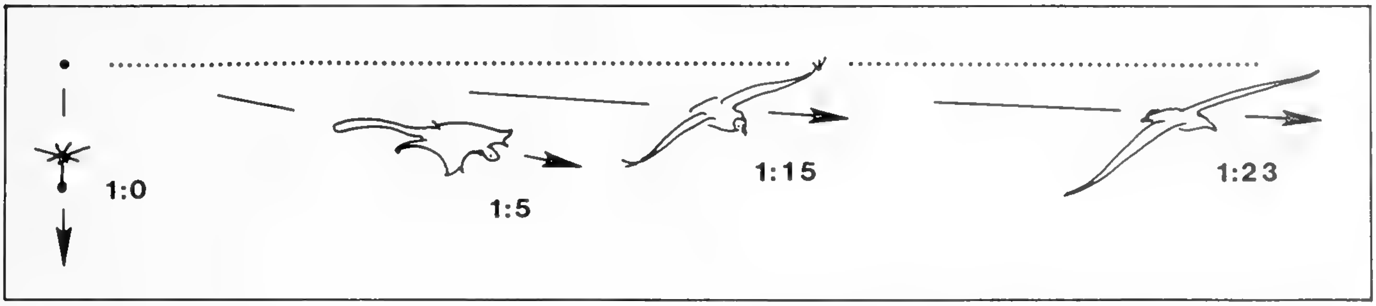

FIGURE 4. Gliding angles drawn to scale for a dandelion seed (straight down), a flying squirrel (1:5), a condor (1:15), and a wandering albatross (1:23).

less likely that flight would originate in a running and leaping animal, as suggested by Caple et al. (1983), since this would involve a direct transition to strenuous low-speed flight, besides requiring difficult coordination requirements to be met de novo, without an existing basis of flight adaptations. A gliding animal can already control itself in a steady glide, and has only to build on this by supplying a minute amount of power from its muscles, so slightly flattening the gliding angle. Some form of selection pressure is needed to make it advantageous for a gliding animal to do this, and then to continue increasing the amount of power supplied from the muscles, until the glides finally merge imperceptibly into horizontal, powered flight.

Arboreal Gliding as the Basis of Foraging

A recent study by Scholey (1985) of an Asian flying squirrel, *Petaurista petaurista,* sheds new light on the ecology of these arboreal gliders. Although this particular animal is rather large to be a flying ancestor, its habits suggest a route by which a smaller, similar animal could have made the transition to powered flight. *Petaurista petaurista* has a body mass of about 1.3 kg, a very high wing loading of about 120 N m^{-2} (similar to that of large albatrosses), and a very low aspect ratio of about 1.5. Its method of flight consists of dropping steeply for about 7–8 m to pick up speed, then leveling out in a steady glide at a speed of about 15 m s^{-1}, descending at an angle of about 12°, or 4.8:1. Part of the initial drop is recovered when the animal pulls up before landing in a head-up posture on a tree trunk (Fig. 5). It then runs vertically up the trunk, regaining the height lost in the glide, prior to another takeoff. This sequence, repeated from tree to tree, is the basis of the animal's foraging behavior. Each individual has a fixed roosting hole from which it emerges at dusk, and then proceeds in a series of glides to a feeding area, returning in the same manner before daylight to the roost. A large fraction of both the time and the energy required to travel across country by this method must be consumed in the vertical climbs up tree trunks. Scholey's figures imply that over 200 m of vertical climbing is required for each kilometer the animal travels across country. Clearly any adaptation that reduces the amount of climbing will increase the speed of travel. This in

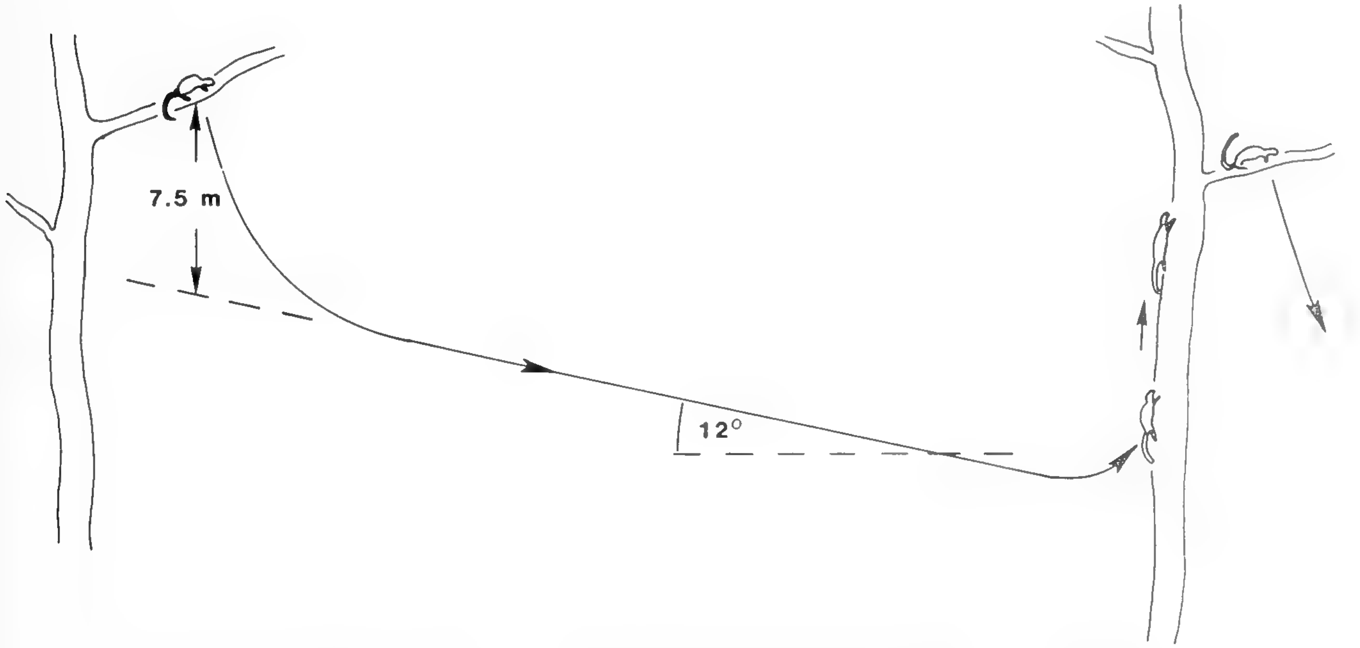

FIGURE 5. Sequence of climb and glide in a foraging flying squirrel *Petaurista petaurista*, as described by Scholey (1985).

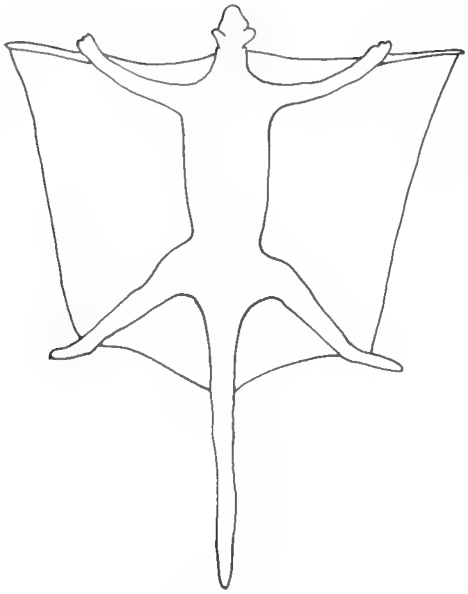

FIGURE 6. Planform of *Petaurista petaurista*. From Scholey (1985). The wing tip is supported by a cartilaginous spur, projecting from the wrist

itself might be sufficient to cause such an adaptation to evolve, since an increase in cross-country speed would increase the area accessible to the squirrel in the course of a night's foraging, and this might in turn significantly increase the reliability of its food supply.

Pressure for Elongation of the Wing

One type of adaptation tending to flatten the glides is elongation of the wing. Figure 6 shows *Petaurista* in flight, extending its modest wing span with the aid of cartilaginous spurs on its wrists. Other gliding mammals have different structures that have much the same effect. It seems to be difficult to elongate the forelimb itself, presumably because this slows down the vertical climbing action on tree trunks, or makes it less efficient. Elongation of the wing can only continue to a point at which the gain in flattening the glides is offset by the loss of climbing ability. This creates a barrier which has to be overcome before the wing can be elongated further. Modern patagial gliders seem to extend the wing to an aspect ratio of about 1.5, and stop at that point.

Pressure for Oscillation of the Wing

An alternative method of flattening the glide is to use muscle power to generate thrust. Any type of repetitive muscle contraction, which has the effect of imparting momentum to the air backwards along the flight path, will result in some forward thrust, and hence flatten the gliding angle (Fig. 7). This thrust would initially be very small, and work would have to be done at a rate equal to the thrust times the forward speed. The exact method by which this work is generated does not affect the argument, but one may assume that in the ancestors of the birds, bats, and pterosaurs, it came from very small contractions of the pectoralis muscles. The effect of the forward thrust is *not* to increase the gliding speed but to flatten the gliding angle. This leads indirectly to an increase in average cross-country speed, by reducing the time spent in climbing.

Apart from this increase of cross-country speed, exerting power in the glides may or may not also result in a saving of energy. The effect of flattening each glide is to shorten the following climb, so saving some energy during the climbing phase, but this is achieved at the expense of supplying some work from the muscles during the glide. If the small amount of energy saved exceeds that expended in the gliding phase, then this alone would supply selection pressure for the further development of the flapping mechanism. This is not essential, as the selection pressure could also be based on the saving of travel time resulting from shortening the climbs. Either way, as the process continued, with progressively more power supplied in the glides, and shorter climbs, the climbing phase would gradually dwindle to a minor part of the total locomotor activity. There would then no longer be any obstacle to elongation of the wing beyond the shape typical of flying squirrels. Lengthening the wing would further flatten the glide, leading finally to an animal with fully developed wings, capable of horizontal flight.

Origin from Quadrupedal Gliders—Bats and Pterosaurs

An animal resembling *Petaurista* could extend its wingtip by elongating the most posterior finger, instead of developing a special cartilaginous spine as shown in Figure 6. It is easy to see how such an arrangement could have led to the type of wing seen in pterosaurs. The dermopteran *Cynocephalus* is another forest glider that shows a strong general convergence on *Petaurista,* but differs from it in some minor, but potentially significant details. In particular, its wing membrane extends to the finger tips, and forms a web enclosing the fingers. Elongation of the fingers from a starting point of this type could lead to the type of wing seen in bats, in which the membrane is supported by several fingers, instead of only the last. Either type of development is readily conceivable from quadrupedal gliding animals. The first stage in developing a wing in such animals is to stretch a lateral patagial membrane between the fore- and hindlegs. The hindlegs are from the start an integral part of the wing support and are likely to remain so during further developments. It is maintained here that this is true of both bats and pterosaurs, contrary to some recent reconstructions of pterosaurs (below).

Mechanics of the Bat Wing

Studies of the way bat wings work have implications, which have not always been appreciated, for the reconstruction of pterosaurs. Figures 8 and 9 are diagrams of a gliding fruit bat, *Rousettus aegyptiacus,* from Pennycuick (1973). This animal is a small pteropodid with a body mass of 0.12 kg, wing loading of 24 N m^{-2}, and maximum aspect ratio of about 5.5. It was trained to glide in a tilting wind tunnel, and photographed perpendicular to the air stream with a stereoscopic camera. Stereo pairs of photographs were analyzed in a map-making machine to produce contour maps of the wings, with contours spaced at intervals of 1 cm below the camera (Fig. 8, 9). At the right of each diagram is a set of chordwise sections through the wing, derived from the contoured plot. In Figure 8 the bat is gliding near its minimum speed, with a lift coefficient of about 1.3. The

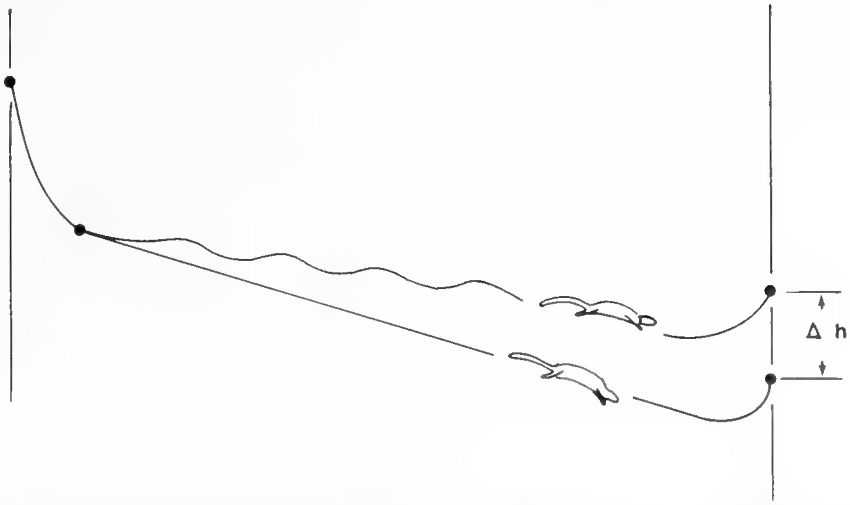

FIGURE 7. A hypothetical flying squirrel which oscillates some part of its anatomy during the glide, in some way that generates forward thrust. In so doing it expends some energy on muscular work, but also saves the time and energy that would have been needed to climb the distance Δh.

wing is fully extended, with a convex profile shape (bulging upwards) over the whole membrane. The profile shape of the distal part of the wing is controlled by the fingers, but that of the plagiopatagium (the large posterior panel of the wing) is controlled mainly by the legs. Flexure of the ankle joint is used to produce a downward curl along the trailing edge of the plagiopatagium. The legs are an essential structural element of the wing for two reasons—they support the proximal end of the membrane and also control its profile shape.

Figure 9 shows how the profile shape of the membrane is modified to fly at higher speeds, in this case at a lift coefficient of about 0.49. The profile shape is flattened by contraction of the plagiopatagialis muscles, which run chordwise in the plagiopatagium without attaching to the skeleton at either end. An area of reversed camber appears in the plagiopatagium, but the profile shape continues to be controlled mainly by the legs. The downward curl at the trailing edge, caused by deflection of the ankle joints, is still present. Although the performance of the wing is most easily measured in gliding, the function of the legs, in controlling its shape and supporting the inner end of the membrane, is no less important in flapping flight.

Mechanics of the Pterosaur Wing

In recent years a number of authors, notably Padian (1979) and Wellnhofer (1982), have reconstructed pterosaurs with a very narrow, pointed wing shape, having the proximal end of the membrane attached to the side of the body, but not to the legs. This notion derives from fossils in which the wing membranes are clearly preserved, especially the extensive series of rhamphorhynchoid fossils described and illustrated by Wellnhofer (1975*a, b, c*). However, Wellnhofer's illustrations show well-preserved membranes only in the distal part of the wing. The membranes become indistinct proximal to the elbow joint, and they cannot actually be seen joining either to the legs or to the body. The outer part of the wing must have been robust and leathery, as Wellnhofer (1975*c*) says, but it would appear that this was not true of the proximal part. An alternative possibility is that the proximal end of the membrane was attached to the leg, as has traditionally been assumed, but was much thinner and more delicate than the outer part and therefore not preserved in the fossils. This idea has further implications which suggest an altogether different reconstruction of the wing (below).

These fossil wings have been compared to bird wings, with the suggestion that the membranes contained internal stiffening elements analogous in function to a bird's feather shafts, but there are difficulties with this view. The outer wing membranes show a pattern of very fine surface ridges, which Wellnhofer interprets as internal stiffening "fibers," but the arrangement of these "fibers" is very different from that of the feather shafts of a bird's wing (Fig. 10). The "fibers" do not traverse the full width of the membrane, are not visible in the proximal part of the membrane, and are not visibly connected to the skeleton. In view of the massive size of the wing finger, it is unclear in any case what loads they would have been required to carry. Another possible interpretation of the "fibers" is that they are not structural elements at all, but wrinkles in the skin, caused by the contraction of internal elastic fibers, oriented *transversely* to the ridges, which would then only appear when the wing is relaxed. Figure 11 represents an alternative reconstruction, postulating a wing in which the outer part is robust and contains elastic fibers while the inner part is thin and delicate and thus not preserved in the fossils. Figure 11 takes account of Padian's (1983*a, b*) view that the legs moved parasagittally as in birds (rather than being rotated round dorsally as in bats), although an upright bipedal stance for pterosaurs is ruled out on other grounds (below). This reconstruction is also reconcilable with Wellnhofer's opinion that there was no pubic symphysis, which would have resulted in the legs being somewhat splayed laterally. It accounts for the modified fifth metatarsal, for which neither Padian nor Wellnhofer were able to suggest a function, by assuming that this provided an anchor point for a robust trailing-edge tendon. It is suggested that this tendon stretched the elastic fibers against the forward pull of the wing finger, which was itself protracted by a muscle originating on the expanded anterior process of the head of the humerus. This process is otherwise

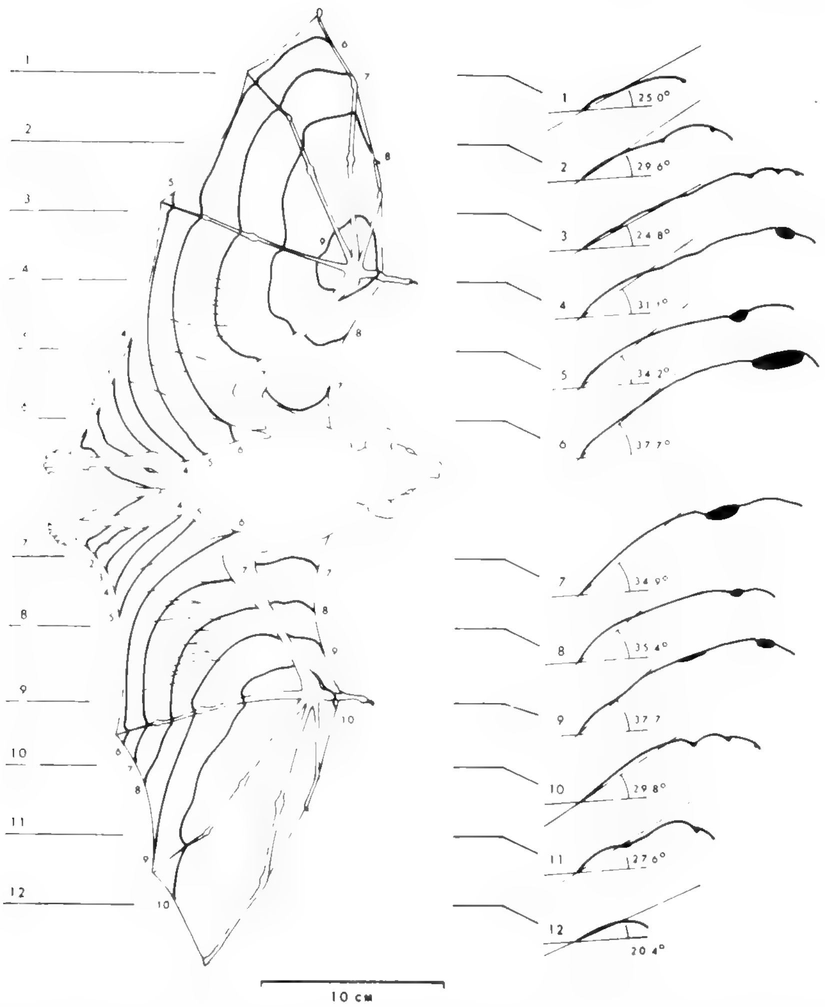

FIGURE 8. Contour map of a pteropodid fruit bat *Rousettus aegyptiacus* gliding in a wind tunnel, from Pennycuick (1973). The leg supports the inner end of the plagiopatagium, and controls its camber. Cross-sections are shown at right. The bat had a mass of 0.12 kg and a span of 0.52 m. It was here flying at an airspeed of 5.45 m s^{-1}, a lift coefficient of 1.27, and a Reynolds number of 34000.

anomalous, because if it were the insertion of the pectoralis muscle, as Padian (1983*a*) assumes, the wing would have been pronated much more strongly than in birds or bats. However, if this process served as the origin for a special extensor muscle, as suggested here, the pectoralis could have inserted in much the same position as in other flying vertebrates.

With the wing spread to its maximum area (Fig. 11A) the surface wrinkles ("fibers") would be smoothed out and disappear. Relaxation of the extensor muscle (Fig. 11B) would allow the outer part of the wing to be swept back, with the elastic fibers contracting to maintain the tension against the tendon and hence keeping the thin proximal membrane stretched out. The ability to sweep back the hand-wing in this way is also seen in birds, which achieve it by flexing the wrist joint and increasing the extent of overlap between the primary feathers. Birds do this in order to trim to higher speeds in gliding (Pennycuick 1968) and also to reduce the wing span in the upstroke of cruising flapping flight. The postulated pterosaur wing would have been functionally nearly equivalent to a bird wing. Bats, on the other hand, are much more limited in their ability to vary wing planform, because retraction of a bat's hand-wing removes the tension from the inner part of the wing (Pennycuick 1971). They trim to high gliding speeds by controlling profile shape rather than planform (above).

It may be noted that the wing shown in Figure 11 has an aspect ratio of 7.1 when fully extended, which is a typical value for small to medium-sized birds and bats. Reconstructions in which the inner end of the membrane is attached to the side of the body, and not to the leg, have the narrow, pointed shape of the dead wings (Fig. 10). Their aspect ratios are much higher than those evolved by living animals of comparable size, besides allowing little or no facility for controlling planform or profile shape.

Ancestral Forms

The proposed pterosaur wing is very different functionally from a bat wing but resembles it in that the bending strength resides entirely in the skeleton, the main lifting surface is flexible with no inherent stiffness, and tension has to be maintained

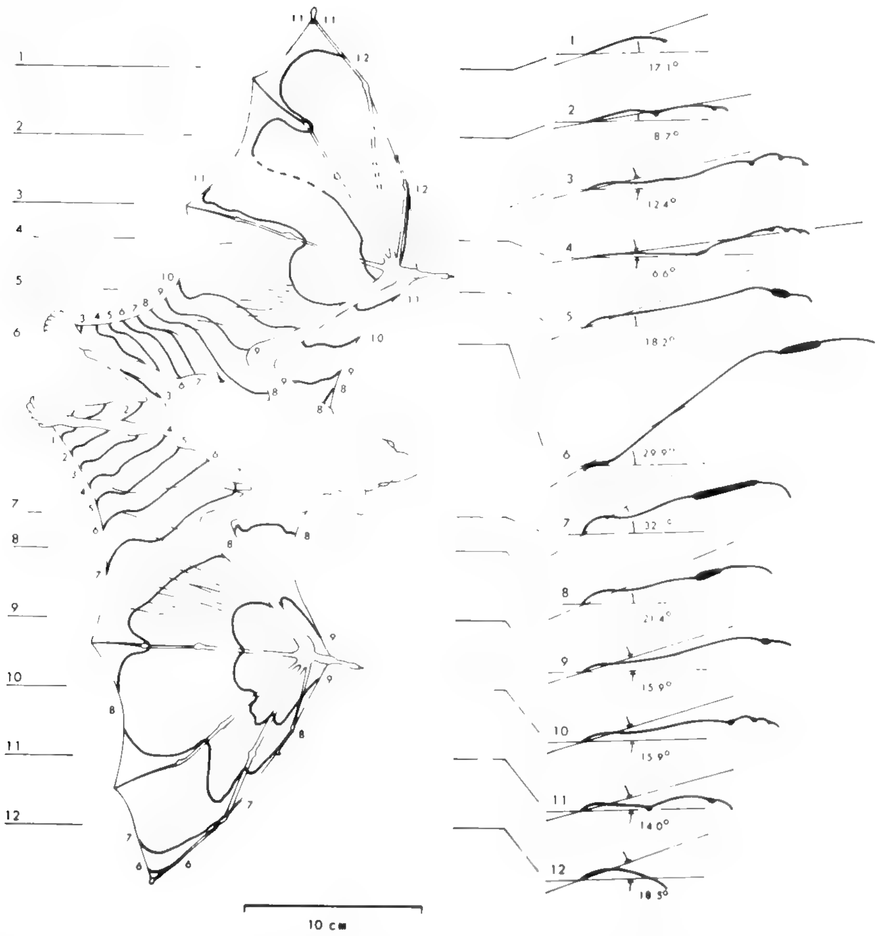

FIGURE 9. The same bat as in Figure 8, flying at an airspeed of 9.00 $m\ s^{-1}$, a lift coefficient of 0.49, and a Reynolds number of 57000. The planform is little altered, but the profile shape is flattened by contraction of the plagiopatagialis muscles. The leg still supports and controls the shape of the inner end of the membrane.

between the arm skeleton and the leg. These characteristics are readily understood if both groups were descended from arboreal patagial gliders, with a general resemblance to flying squirrels. It is proposed here that bats originated from small, arboreal insectivorelike ancestors that developed patagial gliding, then added power as suggested above. Pterosaurs show specializations of the leg skeleton that Padian (1983*a*, *b*) interprets as cursorial adaptations, but as these were presumably inherited from a cursorial archosaur ancestor, their presence does not necessarily imply that pterosaurs remained cursorial. This cursorial ancestor, it is proposed, gave rise to small, secondarily quadrupedal, arboreal forms, which then developed patagial gliding and gave rise to the pterosaurs, still retaining signs of their cursorial origin.

Origin from Bipedal Gliders—Birds

Featherless Gliding Precursor of *Archaeopteryx*

To account for the origin of birds by a similar route, we have to assume that *Archaeopteryx* and its ancestors were bipedal arboreal gliders. Regrettably, no living examples are known of this type of adaptation, but some of its attributes can be inferred. The ancestors of *Archaeopteryx* were presumably gliders before they had feathers. A likely wing for this prefeather phase might be one with a propatagium, but no plagiopatagium, as suggested in Figure 12. The three long, slender and otherwise unspecialized fingers of *Archaeopteryx*, illustrated by Swinton (1960) and Ostrom (1974, 1976), were evidently not firmly bound to the flight feathers, and their function has never been satisfactorily explained. They could have supported a small, batlike hand-wing, constituting the main wing area in the stage before feathers were developed. The legs would have remained free of the wing membrane and would have been able to evolve independently for bipedal locomotion and other functions such as manipulating food.

A wing of the type shown in Figure 12 would have a higher aspect ratio and smaller area than that of a modern, quadrupedal gliding mammal. This hypothetical animal would therefore glide faster and at a flatter angle than a flying squirrel of similar mass. Its height gains might be made by climbing vertically up tree trunks like a woodpecker, in the manner analyzed by Winkler and Bock (1976), or perhaps more laboriously, by hopping and clambering up through the branches. At small sizes (tens of grams), one can imagine such an animal gliding in much the same way as *Draco*, controlling its flight by inertial movements of its long whiplash tail. At larger sizes it would become unduly

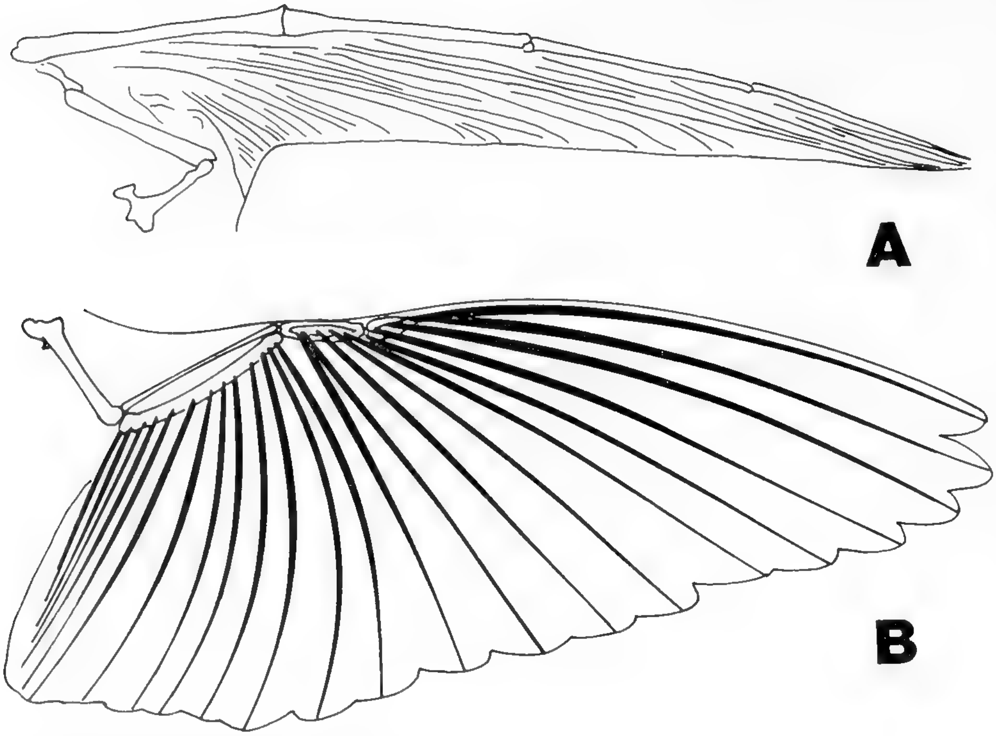

FIGURE 10 The bending strength in a bird's wing (B, pigeon) resides in the feather shafts, which are radiating, tapered spars, robustly supported at their proximal ends, where the bending loads are transferred to the short, thick arm skeleton. In pterosaur wings (A, *Rhamphorhynchus muensteri,* based on Plate 17 of Wellnhofer 1975*b*), the wing finger forms a massive spar extending to the wing tip. The "fibers" described by Wellnhofer are too fine to be shown at this scale, but they lie roughly parallel to the coarser lines shown, which are presumably folds in the membrane. Both "fibers" and coarse folds suggest internal elastic fibers, oriented as in Figure 11, pulling the dead wing into a narrow, contracted shape. The pattern of folds is unlike the radiating pattern of a bird's feathers. The individual folds or "fibers" do not taper like feather shafts and are not arranged in a suitable way for transferring bending loads to the arm skeleton.

fast, because wing loading, on which gliding speed depends, scales like the one-third power of the mass. At the size of *Petaurista petaurista,* this animal would require a very long drop at take-off, and would then glide at a formidable speed.

Evolution of Feathers

The addition of flight feathers along the posterior margin of the wing must have been an adaptation to increase the wing area, and thus reduce the gliding speed. It would also entail some loss of efficiency, because of the reduced aspect ratio, though not, of course, to the degree of inefficiency seen in flying squirrels. An adaptation to reduce speed may seem paradoxical, but it can be understood in terms of a need to shorten the drop at takeoff and to increase maneuverability when weaving among the branches. This need would make itself felt if there were a tendency for the size of the animal to increase, say from a few grams up to the size of *Archaeopteryx.* Such an increase in size would entail an increase of wing loading, and hence of gliding speed, if all dimensions were kept in proportion. A disproportionate increase in wing area would be needed to keep speeds down.

The increased area was evidently provided by enlarging the scales along the posterior margin of the wing. The reason for having scales on the wing in the first place would most probably be to protect the patagium from the sun (below). As noted by Parkes (1966), this solution, once initiated, would require additional stiffening of the scales, leading to a ridged pattern from which flight feathers could easily be derived (Fig. 13). Unlike a patagium, which must be stretched between two skeletal supports, scales along the posterior margin of the front limb would be attached only at their anterior ends and would tend to bend upwards under the air pressure. A longitudinal stiffening rod would have to be developed to resist this tendency, but the lateral vanes would still tend to curl upwards. Further stiffening ridges would be needed, resembling the pattern of barbs in a modern feather. The final stage, the separation of these ridges into barbs, appears already to have been reached in *Archaeopteryx,* of which some of the feather impressions show the barbs separating, as in modern feathers. The development of down feathers as thermal insulation is a separate process that may or may not have preceded the development of flight feathers.

FURTHER ADAPTATIONS OF FLYING VERTEBRATES

The Dual Locomotor System of Birds

A bat or flying squirrel has to use all four limbs when flying, and also when walking or climbing. Adaptation of the limbs to improve one mode of locomotion inevitably has an adverse effect on their performance in the other. No such limitation applies to birds, which fly with their wings alone. Birds' legs serve supplementary functions in slow flight, but in cruising flight they are usually trailed behind, or tucked up under the flank feathers. Conversely, a bird on the ground walks or runs on its legs only and can keep its wings folded up. Birds typically

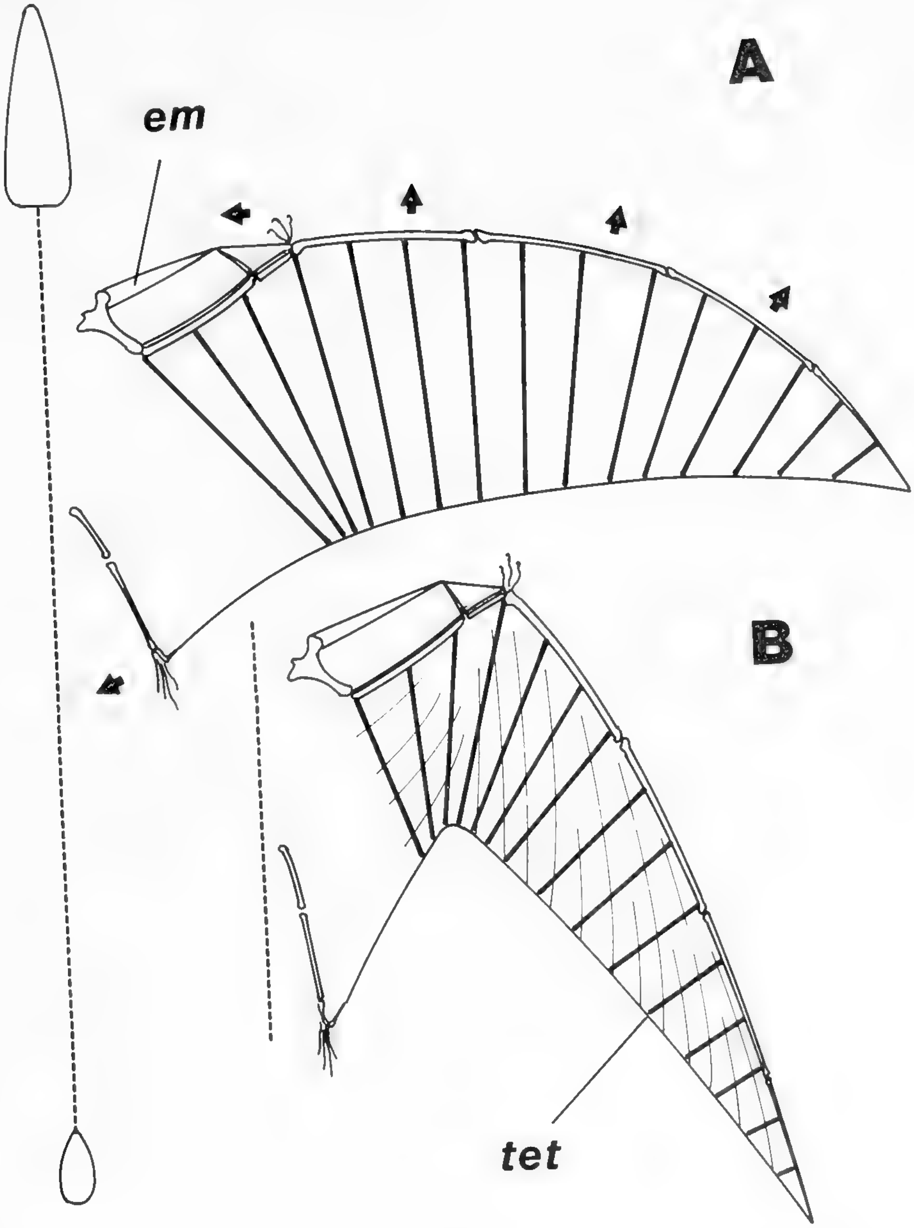

FIGURE 11. Hypothetical reconstruction of a pterosaur wing, based on *Rhamphorhynchus muensteri*. The lengths of the bones, and the distance from shoulder to hip joints, have been taken to scale from the complete skeleton illustrated in Plate 20 of Wellnhofer 1975*b*. The thick lines represent hypothetical elastic ligaments stretched between the wing finger and a trailing-edge tendon (tet), which runs from the wing tip to the fifth toe. The wing finger is protracted by a postulated extensor muscle (em) originating on the prominent anterior process of the head of the humerus, which would otherwise be anomalous. Relaxation of this muscle would allow the hand-wing to be swept back and reduced in area (B), as in birds, without collapsing the proximal part of the membrane. The length of the tendon is the same in A and B. The pteroid bone is tentatively interpreted as a compressive element, as suggested by Frey and Riess (1981).

have two independent locomotor systems, of which only one is used at a time.

This independence of the fore- and hindlimbs allows each to be adapted for a different form of locomotion, without affecting the other. Usually the legs continue to function in a basically dinosaurlike manner for walking, hopping, or perching, while the wings are used for flight. Alternatively, many water birds use their legs for a combination of walking and swimming (gulls, ducks, cormorants, etc.), whereas others (auks, diving petrels) use their wings to combine flying and swimming. Penguins use the wings for swimming alone and the legs for walking. Many birds can perform in two entirely different modes of locomotion, or even three, with a degree of efficiency that is competitive with other animals having only one. The spectacular versatility of birds in combining different modes of locomotion is achieved with only trivial modifications to the leg and wing skeletons. The operation of the legs and wings is much the same in all birds, including flightless forms. Adaptations to widely different types of locomotion are achieved by variations in the shapes and relative sizes of a standard set of parts.

FIGURE 12. Hypothetical ancestor of *Archaeopteryx,* before the development of feathers. The three elongated fingers, still present in *Archaeopteryx,* support a propatagium and a batlike hand-wing. There is no plagiopatagium, as the leg is still used for bipedal locomotion and is therefore not available to support it.

The Bird Synsacrum—the Pelvic Lever

Although the legs of birds are dinosaurlike, the pelvis is not. Mechanically, the bird synsacrum is a long channel girder, folded in such a way that it resists dorsoventral bending. Its function is easily understood if the position of the acetabulum in a standing bird is considered (Fig. 14). The acetabulum is too far back for there to be any possibility of the center of mass of the body being positioned directly over or under it. A standing bird therefore has a tendency to topple forward about its hip joint, and this has to be resisted by tonic muscles pulling the ischium towards the femur (T in Fig. 14)—hence the long synsacrum, stiffened in a way that allows the downward pull on the posterior end to hold the anterior end up. The problem arises from the loss of the tail in birds. Animals with a long tail, including bipedal dinosaurs, kangaroos, and *Archaeopteryx* can balance their body weight about the hip joint, and therefore do not need to use a pelvic lever to maintain their posture as modern birds do.

The pelvis in early pterosaurs was much the same size as that of *Archaeopteryx,* and they had tails that could conceivably have balanced the weight of the body in a birdlike bipedal posture. The later pterodactyloids lost the tail but did not develop an expanded synsacrum in any way comparable with that of birds. Although there was fusion of pelvic elements and vertebrae, which could technically be regarded as a "synsacrum," the size of this structure, relative to that of the whole body, was similar in tailed and tailless forms. Pterodactyloids did not have the lever arrangement seen in birds, where the synsacrum is enormously expanded, typically extending more than half the length of the trunk (Fig. 14). Bipedal running takeoff is conceivable in pterodactyloids, as suggested in Figure 14, but they could not have supported their weight on the hindlegs without help from the wings and therefore must have walked or clambered quadrupedally as illustrated by Bramwell and Whitfield (1974). It is simplest to assume that rhamphorhynchoids were also quadrupedal, and descended from an arboreal gliding ancestor resembling a flying squirrel (above).

Ventilation

The curved shape of the bird synsacrum preadapts it to another function. It forms a curved plate at the top of the body cavity, facing an oppositely curved plate, the sternum, below it. The two are connected by ribs and ventral ribs, and the joints between these can be flexed and extended by the intercostal muscles. The sternum and synsacrum act as the two halves of a bellows, pumping air in and out of the respiratory system (Hughes 1965). This arrangement pumps air in and out of the entire body cavity (rather than just the thorax as in mammals and crocodiles) and is essential for operating the avian arrangement of air sacs distributed around the whole body cavity. The rib cage could have operated in the same manner in pterosaurs, and they had some pneumatic bones, suggesting that they may have had an air sac system similar to that of birds.

Thermoregulation

A gliding animal may regulate its temperature either endothermally, as in *Petaurista,* or ectothermally, as in *Draco.* Gliding as such does not raise any new problems of thermoregulation. Flapping flight, however, as it gradually develops, introduces a considerable amount of exertion, with a resulting need to dispose of waste heat. A patagial flyer has a ready-made solution to this problem. The patagium is extended in flight and exposes a large surface to the air, from which heat can be carried away by convection. When the animal is at rest, the wing is folded up, and is not exposed to unwanted cooling. Bats, being endo-

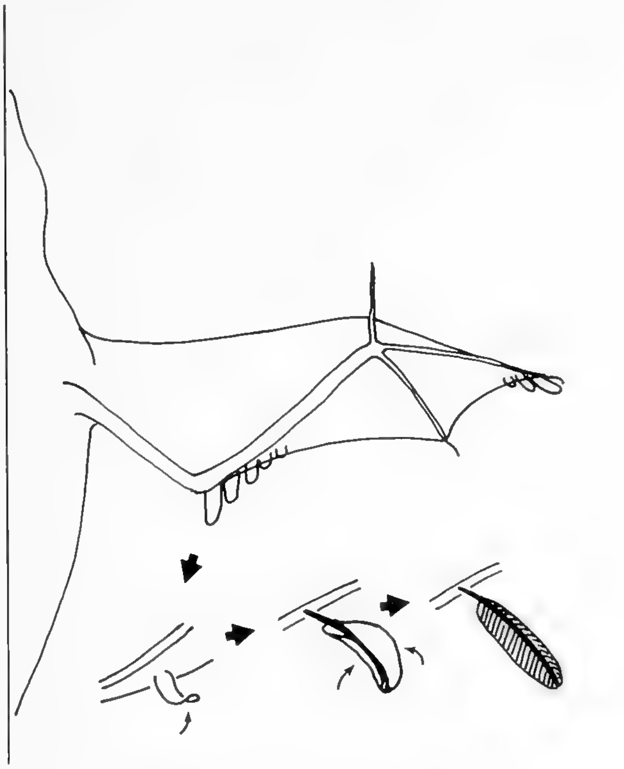

FIGURE 13. Hypothetical development of the wing shown in Figure 12, with enlarged scales increasing its area and span. These scales would tend to curl upwards under the air pressure, so requiring a central stiffening rhachis, supplemented by lateral stiffening ridges to prevent the vanes from curling up at the sides.

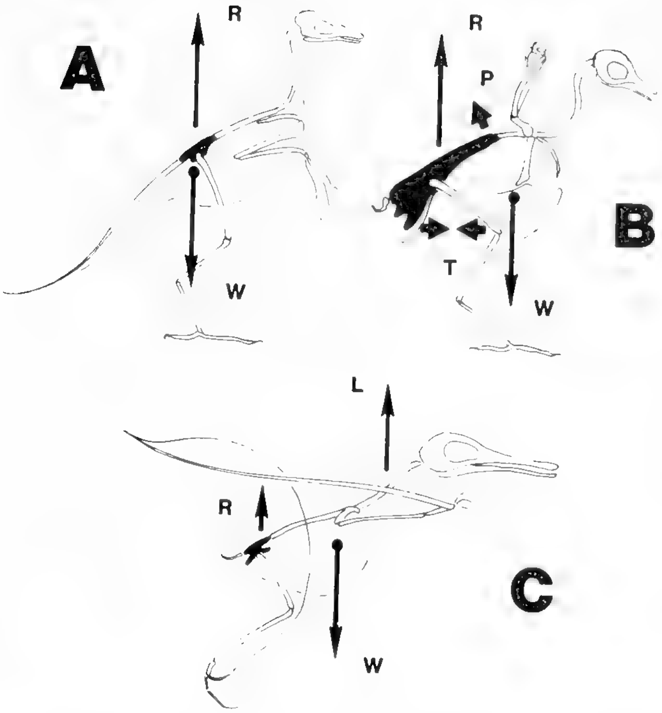

FIGURE 14. In *Archaeopteryx* (A) the long tail would have allowed the body weight (W) to act along approximately the same line as the upward reaction from the hip joint (R). Modern birds (B) have lost the tail, and the body weight therefore acts ahead of the hip joint, tending to topple the body forward. This is resisted by the enormously expanded, shoehorn shaped synsacrum, which works as a lever. Tonic muscles (T) pull the posterior end of the synsacrum towards the femur, and this in turn holds the anterior end of the body up (P). The later pterosaurs (C, based on *Pterodactylus* as illustrated by Romer 1945) also lost the tail, but did not develop a similarly expanded synsacrum. They had no adaptation which could have allowed moments to be balanced about the hip joint in bipedal standing. A running take-off might have been possible, as shown, with part of the weight supported aerodynamically (L) by the wings.

thermal regulators, have hair on their bodies but not on their wings. The wings do not require insulation because their function in thermoregulation is to dispose of excess heat.

The convective cooling system of bats only works if the air is substantially cooler than the blood. Bats are therefore mainly crepuscular or nocturnal animals, flying when air temperatures are low and there is no radiant heat load from direct sunlight, to which the wing membrane is sensitive. Birds do not have these limitations, because they can resort to evaporative cooling at higher temperatures, and the feathers protect the skin from direct sunlight. If pterosaurs relied wholly on convective cooling, they would have suffered the same limitations as bats, but if they had an air sac system which could be used for evaporative cooling, then they too would have been able to fly at higher ambient temperatures. Sharov (1971) has described a pterosaur (*Sordes pilosus*) in which the integument is preserved, with dense, hairlike fibers on the body and a sparse covering of fibers on the wings. The latter would be difficult to account for in terms of thermoregulation, but if the animal was diurnal, they could have served to protect the patagium from sunlight. It may be added that Prof. Walter Bock (pers. comm.), who has seen this fossil, has expressed some doubts as to whether the fibrous structures really are hair or any form of thermal insulation.

Evaporative Cooling and the Bird Carina

Birds also lose heat by convection in flight, both from the under surface of the wings and from the sides of the body, which are covered when the wings are folded (Eliassen 1962). The area available for cooling is, however, much smaller than in bats. Convective cooling is effective when the ambient air is cold, but has to be supplemented by evaporative cooling at high air temperatures (Tucker 1968). A unique feature of birds is that they are able to cool their flight muscles directly, without having to remove heat via the bloodstream. Branches of the interclavicular air sac ramify inside the flight muscles, providing an internal evaporation surface from which the water vapor can escape to the outside through the bronchal system. This is the reason for the prominent bony carina on the sternum of flying birds. It prevents the pectoralis muscles from collapsing their internal air cavities when the muscles contract (Fig. 15). Bats use a different method of cooling, in which heat is removed from the muscles by the blood and carried to the wings, where it is disposed of by convection (Reeder and Cowles 1951). Having no air cavities in their muscles, bats do not need a carina. The pectoralis muscles of a bat pull directly against one another, without needing a bony support in between. No carina can be seen in the *Archaeopteryx* fossils, implying that this animal did not have air cavities in its pectoral muscles and perhaps did not have air sacs at all. It could have been an arboreal glider, with no need for additional heat disposal from its muscles. It could even have been ectothermal, like *Draco*, with no thermal in-

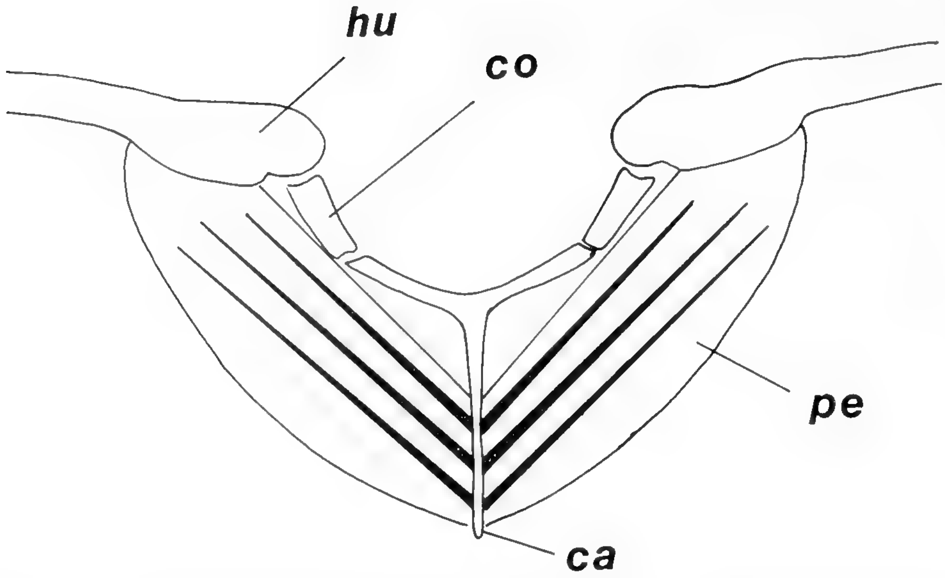

FIGURE 15. Schematic transverse section through the pectoral muscles and shoulder joints of a bird. The muscle contains air cavities (solid black), which are connected to the interclavicular air sac, and can remove heat by evaporation directly from the interior of the muscle, without the intervention of the blood stream. The carina of the sternum prevents these cavities from collapsing when the muscles contract. Bats do not have air cavities in their muscles, and therefore do not need a carina. hu = humerus, co = coracoid, ca = carina of sternum, pe = pectoralis muscle.

sulation. Pterosaurs also lacked an expanded ossified carina comparable with that of birds, which implies that if they had air sacs, they did not use them for directly cooling their pectoral muscles. A hypothetical cartilaginous extension of the carina, as suggested by Padian (1983*a*), would not have served the same function. Because of the steep angle at which the pectoralis fibers are attached to the sternum, the carina has to resist strong compression, for which bone, not cartilage is required. Absence of a bony carina does not necessarily imply that the flight muscles of pterosaurs or *Archaeopteryx* were weak, only that there was no requirement to resist compression.

Cursorial to Arboreal Sequence

The best living examples of cursorial bipedal animals are the ratites, which are all much too large to fly. Most of the known cursorial dinosaurs were at least as large as modern ratites, and many were considerably larger. As noted above, fast bipedal or quadrupedal running seems to work best at these comparatively large sizes. The ratites have evidently relinquished the power of flight as a necessary consequence of evolving the large size best suited to this mode of locomotion. As noted above, a prospective proavis needs to be in the mass range 10–100 g to have the best chance of evolving powered flight, and this is not a favorable range for cursorial locomotion. However, there is one characteristic of birds that indicates that they are descended from a tall ancestor, which may also have been ancestral to dinosaurs and pterosaurs. This feature is the fully divided ventricle.

Divided Ventricle Indicative of a Tall Ancestor

The undivided ventricle, as seen in modern amphibians, and reptiles other than crocodilians, has the advantage that the volume rate of flow through the systemic and pulmonary circulations can be different (Fig. 16). This allows the flow through the lungs to be reduced, while maintaining that through the body, a useful facility in diving and in collecting heat from the body surface during ectothermal warming. The disadvantage is that since the systemic and pulmonary circulations both receive their blood from the same ventricle, it is difficult to supply blood to the former at a substantially higher pressure than to the latter. The maximum pressure that can be contained by the lung capillaries is limited because they are partially surrounded by air and not supported by surrounding tissues, as are capillaries in other organs. The minimum pressure needed to supply the brain depends on the height the blood has to be lifted from the heart to the head. Thus a horizontal reptile can supply blood to its brain without bursting its lung capillaries, but this is difficult for a tall one.

If only static pressures were involved, both the systemic and pulmonary circulations would be supplied at the same pressure (P in the lower diagram of Fig. 16). In fact, living lepidosaurian reptiles can do somewhat better than this. For example, varanid lizards are able to supply blood to the systemic circulation at over twice the pulmonary pressure (Burggren and Johansen 1982). This is apparently achieved dynamically with the aid of a muscular ridge that partially divides the ventricle. However, the pressure in the systemic arch is still less than 10 cm water gauge, which is insufficient for a large, or even medium-sized animal to stand in an upright posture. Seymour and Lillywhite (1976) confined various kinds of snakes in tubes and tilted them into a head-up posture. Snakes in general cannot tolerate this for long periods. Certain arboreal snakes showed a limited ability to compensate for the short-term pressure change, but sea snakes were unable to do so.

A large animal that stands upright for extended periods has no alternative but to divide the ventricle fully (Fig. 16), accepting the inconvenient consequence that the volume rate of flow through the lungs then has to equal that through all other organs combined. The divided ventricle of birds thus indicates that

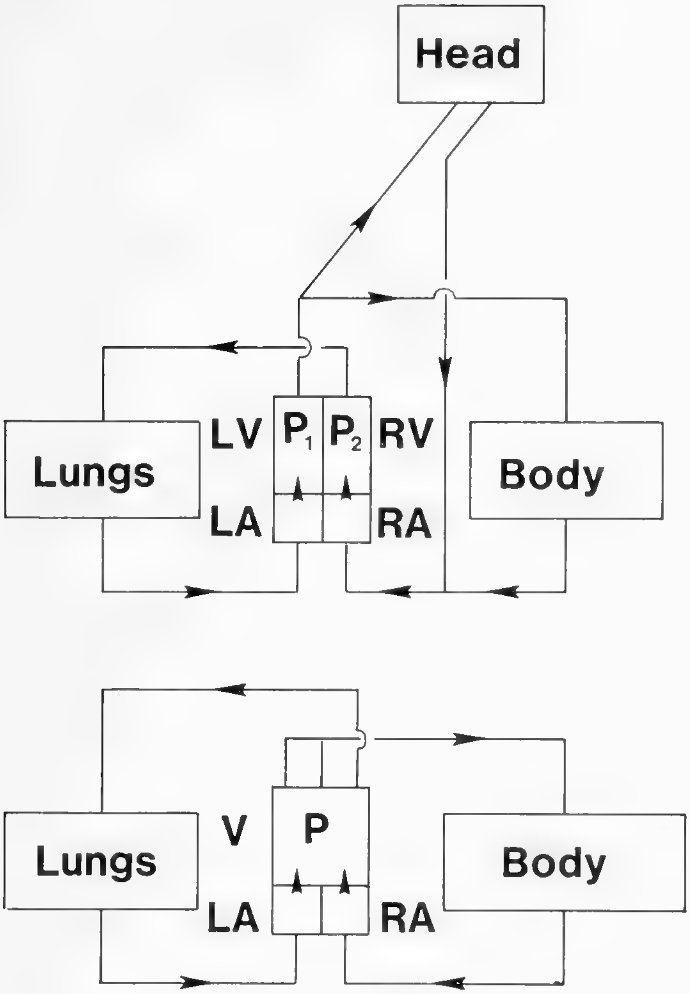

FIGURE 16. In a prone vertebrate (bottom), the ventricle can be undivided. Blood is supplied to both the systemic and pulmonary circulations at the same pressure (P), but the rate of flow in each circuit can be different. In particular, the rate of flow through the lungs can be reduced when these are not in use, as in diving. An upright animal (top) must supply blood at a relatively low pressure (P_2) to its lungs and at a higher pressure (P_1) to lift blood to the head. The ventricle therefore has to be completely divided, and becomes two ventricles. Effectively the animal has two hearts connected in series, so that the rate of flow through each has to be the same. Abbreviations: LA = left atrium, RA = right atrium, LV = left ventricle, RV = right ventricle.

they are descended from a tall ancestor. This could well have been a common ancestor of birds, pterosaurs, and dinosaurs and may be assumed to have been a tall, bipedal, cursorial animal. If that were the case, all three groups would have inherited the divided ventricle from the same source. Similarly, mammals no doubt inherited their fully divided circulation from a tall ancestor in the Permo-Triassic radiation of synapsid reptiles.

Crocodilians, the only horizontal archosaurs, have a fully divided ventricle, but also retain the left systemic arch, and can use it as a pulmonary shunt. This condition is perhaps best seen as a secondary development from a fully divided circulation, rather than an "improvement" of a lizardlike arrangement, as Webb (1979) suggests. Bird embryos have to retain the left systemic arch as a pulmonary shunt and only lose it at the time of hatching. It may be supposed that the adult bird condition is primitive for archosaurs, and the crocodilian arrangement is derived from it by neoteny.

Ancestry of Birds and Pterosaurs

If the common ancestor of birds and pterosaurs had a divided ventricle, it must have been an upright, and most probably cursorial, animal. As noted above, the potential diversity of cursorial animals dwindles rapidly as mass is reduced below about 50 kg, and there is no chance of finding a cursorial animal in the 10–100 g range most favorable for originating flight. Therefore, this earliest ancestor must have given rise to some later forms using other methods of locomotion, which allowed smaller animals to evolve. Most likely these were arboreal forms. The body masses of living arboreal vertebrates range from a few grams in small lizards and frogs up to 100 kg or so for a male orangutan, thus easily bridging the gap between cursorial and flying forms. Cursorial animals can and do take to the trees at times, modern examples being the domestic goat (*Capra hircus*) and the tree kangaroos (*Dendrolagus* spp.).

One may conclude that at some time after the cursorial origin of archosaurs, but before *Archaeopteryx*, there must have been a fauna of small (10–100 g) arboreal archosaurs, within which two contrasting types should be distinguishable, as follows.

1. Some of these forms must have retained bipedal locomotion in the trees. They must have included gliding forms, with a patagium not attached to the legs. Among these would be the featherless, patagial ancestors of *Archaeopteryx* and the birds.

2. Another branch of this archosaur stock must have changed to a secondarily quadrupedal, squirrel-like method of locomotion. This transition does not seem to be difficult, as some living lizards can use either bipedal or quadrupedal locomotion (Snyder 1952). Gliding members of this quadrupedal group would have resembled modern flying squirrels, with a patagium stretched between the fore- and hindlegs. These would have included the ancestors of the pterosaurs.

These two types of arboreal archosaurs would most likely be of late Triassic or early Jurassic age. Their skeletons would be small and delicate, and would probably be preserved only in exceptional conditions like those that preserved *Archaeopteryx*. It remains for paleontologists to determine whether the expected quadrupedal and bipedal variants of small, early arboreal archosaurs did indeed exist.

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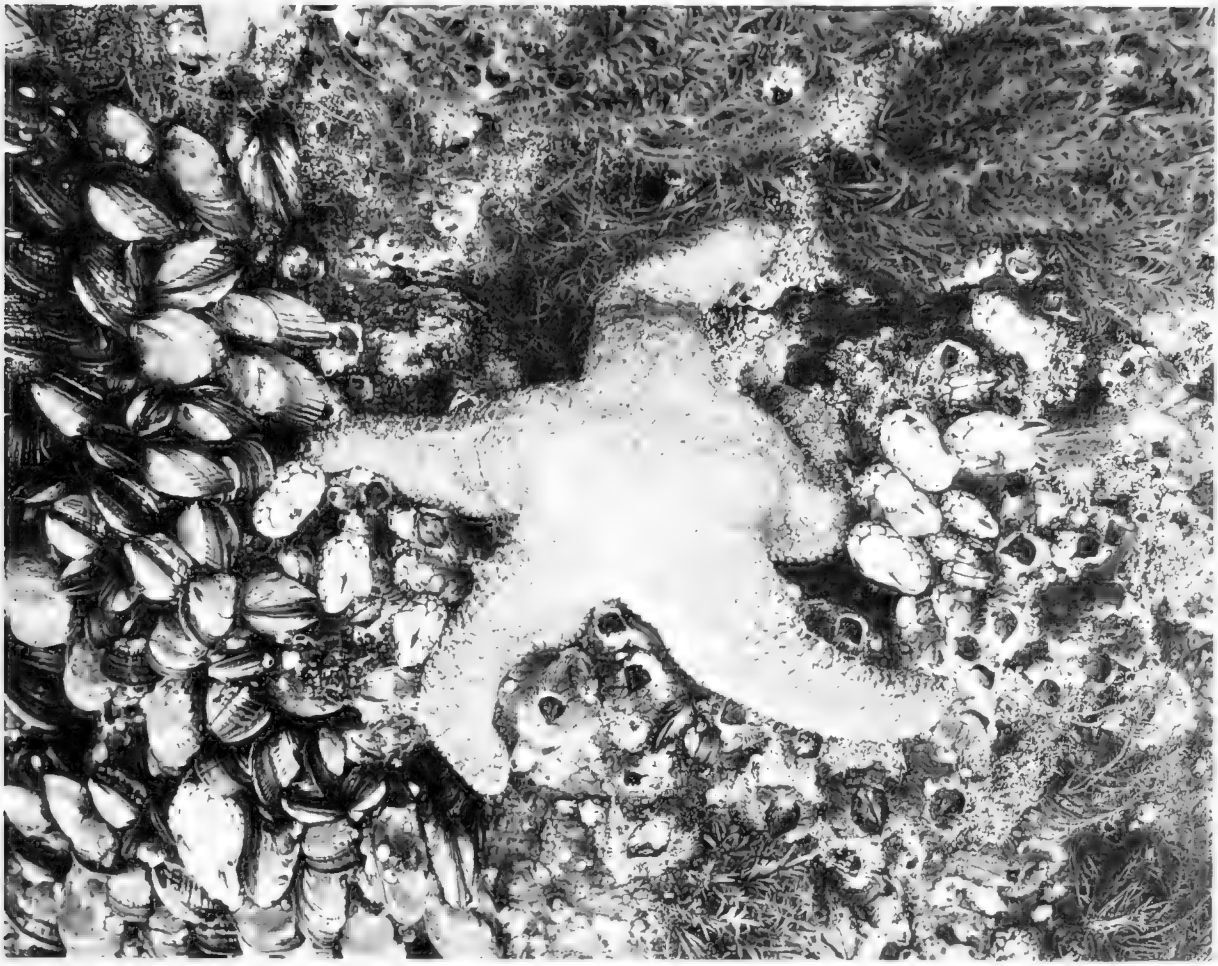
Causes of Spatial and Temporal Patterns in Rocky Intertidal Communities of Central and Northern California

By Michael S. Foster and Andrew P. De Vogelaere, Christopher Harrold, John S. Pearse, Alan B. Thum



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Cover Illustration: Sea star, *Pisaster ochraceous,* feeding on *Mytilus* bed in Monterey Bay, California. Photo by Ralph Buchsbaum. 1981. in The Natural History of Año Nuevo. Burney J. Le Boeuf and Stephanie Kaza, eds. Boxwood Press, Pacific Grove, California.

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... As the years go by I have been more and more impressed by this factor of variation in marine habitats ... it is the change, in other words, the variation shown by these animal communities and the individuals that comprise them which make them so interesting.

G. E. MacGinitie, 1938

I. Introduction

The rocky intertidal biota of central and northern California is among the most luxuriant in the world. The cool, nutrient-rich waters of these shores wash over an extensive array of variable rocky habitats that are particularly favorable for intertidal life. The climate is temperate year around; extreme temperatures, either freezing or torrid, are rarely encountered. The southward-flowing, cool California Current and northward-flowing warmer Davidson Current intermingle in the region, contributing to the unusually equable sea temperatures. Extreme low tides occur in the early mornings during the spring and summer, usually in association with thick fog, so the biota is rarely exposed to overheating and desiccation as is typical of many other shores, especially to the south. In contrast, the extreme low tides in the fall and winter are in the late afternoon, and the biota usually is spared exposure to the occasional, cold morning temperatures. Storms occur mainly in the winter, and these effectively remove accumulated debris and clumps of crowded individuals, creating space for the recruitment and growth of new organisms in the generally calm spring and summer.

The intertidal biota of western North America has had a long and varied history, and species have accumulated over geologic time. There have been repeated invasions of new species as climatic conditions and land forms changed (MacNeil 1965; Durham and MacNeil 1967; Marincovich 1984; Lindberg and Hickman 1986; Lindberg in press). Moreover , in situ speciation events have probably generated new species as interior areas of California were subject to repeated marine transgressions and regressions creating and destroying embayments and islands (Addicott 1969; Vedder and Howell 1980). Species distributions also shifted up and down the coast as the Pleistocene ice sheets advanced and retreated (Valentine 1961), and isolated pockets of the biota provided further opportunity for speciation to occur. On the other hand, mass extinctions during the Pleistocene, such as apparently happened when the shores of the north Atlantic were covered with ice sheets, did not occur in the northeast Pacific. Central California is presently the southernmost part of the Oregonian Province (see Section III.A.1), and many species are near their southern limit in this region. However, many other species of the adjacent San Diego Province to the south extend north into central and northern California. Consequently, the region is a biogeographic zone of considerable species overlap, enhancing diversity.

The biota of central and northern California has been the subject of a variety of descriptive treatments and analyses, as recently summarized by Ricketts et al. (1985), and its organization is relatively well known. The distribution of plants and animals in this biota is influenced by many factors, including tidal level, wave exposure, substrata characteristics (rock type, slope, topography), and to a lesser extent, season. Biotic interactions, such as intra- and interspecific competition and predation, are often intense, leading to a dynamic community organization, and providing a particularly favorable setting for ecological studies (Lewin 1986).

The objective of this review is to summarize present knowledge about the causes of variation in species composition, distribution, and abundance of rocky intertidal plants and animals along the coastline of central and northern California. Examination of the causes of such variation in the intertidal zone, both in space and time, has been the subject of numerous studies in different parts of the world for over 50 years. The most valuable of these studies have included experimental manipulation of populations in the field. However, with important exceptions (e.g., Sutherland 1970, 1972; Haven 1973; Wolcott 1973; Doering and Phillips 1983; Fawcett 1984; Sousa 1984), most of these studies have been done in areas other than central and northern California. Of particular importance to our review is experimental work in southern California (e.g., Harger 1972; Dixon 1978; Sousa 1979*a*, 1980; Taylor and Littler 1982) and Washington state (e.g., Connell 1970; Dayton 1971, 1975; Paine 1974, 1976, 1984; Suchanek 1978, 1981; Quinn 1979; Paine and Levin 1981). Other important experimental work includes that done in New England (e.g., Menge 1976, 1983; Lubchenco and Menge 1978), Great Britain (e.g., Connell 1961*a, b*; Lewis 1977), and southeastern Australia (e.g., Denley and Underwood 1979; Underwood 1980, 1981; Branch and Branch 1981; Underwood et al. 1983). We will attempt to incorporate this work into our discussion below, evaluating how conclusions drawn from it apply to the rocky intertidal zone of central and northern California.

It should be pointed out that much of the descriptive and experimental research, both within central and northern California and elsewhere, has been done near marine research stations—areas that are not necessarily typical of most coastlines. Indeed, most of the shoreline of western North America is remote and inaccessible, and decidedly unsuitable as sites for research facilities. Moreover, even in the vicinity of marine research stations, most intertidal research has been done in selected microhabitats. Flat, gentle inclines often best display intertidal zonation patterns and are the most suitable for setting up experiments that demand replication. Irregular rocky outcrops and boulder fields, more typical of the California rocky intertidal coast (Woodward-Clyde 1982; Hardin et al. in preparation), are rarely examined except for particular species that occur within them (outstanding exceptions are Seapy and Littler's [1978] and Sousa's [1979*a, b,* 1980] work on intertidal boulder fields). Our generalizations about intertidal communities, therefore, must be read with caution, and with full appreciation of the restrictions of the primary research.

Variation in plants is discussed in Section II, and variation in animals in Section III. A general consideration of types and effects of natural and human disturbances on rocky intertidal community structure follows in Sections IV and V, respectively. Variations in space and time are discussed separately within the sections on plants and animals. Relatively little is known about variation in time, and this is reviewed in the appropriate subsections, subdivided into scales of within year (seasonal) and between years (greater than 1 year).

The causes of spatial patterns are reviewed at three scales: geographic, vertical (zonation), and within zone (microhabitat).

TABLE 1. PATTERNS OF ZONATION.

Ricketts et al. (1985) Pacific coast, North America	Carefoot (1977) Vancouver Island, British Columbia	Pearse (1980) Año Nuevo Island, California	Stephenson and Stephenson (1972) Pacific Grove, California	Ferguson (1984) Big Sur Coast, California
LITTORINA KEENAE *Porphyra* *Cladophora* *Enteromorpha* *Ligia* *Balanus glandula*	*PORPHYRA*	SPLASH ZONE Blue-green algae Lichens *Porcellio scaber* *Ligia pallosii* *Littorina keenae*	SUPRALITTORAL FRINGE *Littorina keenae* *Ligia* *Pachygrapsus*	SPLASH ZONE *Littorina keenae* *Littorina scutulata/plena* *Ligia*
BALANUS GLANDULA *Pelvetia* *Littorina scutulata plena* *Tegula funebralis*	BARNACLE ZONE *Balanus glandula* *Chthamalus*			
	MIXED BARNACLES/SEAWEEDS *Balanus glandula* *Gigartina* *Fucus/Pelvetiopsis*	HIGH ZONE *Porphyra* spp. *Mastocarpus papillatus* *Endocladia muricata* *Pelvetiopsis limitata* *Balanus glandula* *Chthamalus dalli* *Mytilus californianus* *Phragmatopoma californica* *Pollicipes polymerus* *Anthopleura elegantissima* *Collisella digitalis* *Collisella scabra* *Tegula funebralis* *Littorina scutulata/plena* *Nuttallina californica*	UPPER MID-INTERTIDAL *Balanus glandula* *Tetraclita*	HIGH ZONE *Porphyra* *Pachygrapsus* *Collisella digitalis/ austrodigitalis* *Collisella scabra* *Lottia*
MYTILUS *Pollicipes* *Nucella californica* *Katharina* *Nuttallina*	MUSSELS/GOOSE BARNACLES *Mytilus californianus* *Pollicipes*	MID-ZONE *Iridaea flaccida* *Anthopleura elegantissima* *Anthopleura xanthogrammica* *Dodecaceria fewkesi* *Collisella digitalis* *Collisella pelta* *Collisella scabra* *Notoacmea scutum* *Tegula funebralis* *Tegula brunnea* *Pisaster ochraceus*	LOWER MID-INTERTIDAL *Chthamalus dalli* *Tegula funebralis* *Thais* *Nuttallina*	MID ZONE *Pagurus* *Tegula funebralis* *Anthopleura elegantissima* *Haliotis* *Lottia* *Katharina* *Mytilus/Pollicipes* (only on offshore rocks)
	BARNACLES/ALGAE *Balanus cariosus* *Ulva* *Halosaccion* Whelks Limpets		INFRALITTORAL FRINGE *Alaria* *Lessoniopsis*	LOW ZONE Sponges Bryozoans Tunicates *Mopalia* *Tonicella* *Leptasterias* *Phyllospadix*
PHYLLOSPADIX Laminarians	*HEDOPHYLLUM* Chitons Sea stars *Phyllospadix*	LOW ZONE *Phyllospadix* *Laminaria* spp *Egregia menziesii* Sponges Bryozoans Tunicates		

Patterns at the geographic and within-zone scales are described in the text. However, because much of the extensive intertidal literature, particularly that published before the 1970s, is devoted to describing patterns of vertical zonation and associated tidal changes, we will only summarize this descriptive information in the following paragraphs, and restrict our review in later sections to the causes of zonation. Ricketts et al. (1985) and Carefoot (1977) provide detailed discussions of zonation patterns, tides, and climate in the northeastern Pacific, Berrill and Berrill (1981) summarize this information for the northwestern Atlantic, Lewis (1964) does the same for the British Isles, and Stephenson and Stephenson (1972) review such patterns for coasts throughout the world. Moore and Seed (1986) review spatial and temporal patterns, with emphasis on the British Isles.

Several schemes of subdividing rocky shores into horizontal bands have been proposed, and the major ones have been reviewed in Ricketts et al. (1985). Included in their discussion of

TABLE 1. CONTINUED.

Seapy and Littler (1978) Cayucos, California (sea stack)	Caplan and Boolootian (1967) San Nicolas Island, California
	LITTORAL FRINGE *Chthamalus fissus* *Littorina keenae*
BALANUS/CHTHAMALUS	UPPER EULITTORAL *Littorina scutulata/plena* *Collisella digitalis*
MYTILUS/POLLICIPES	MIDDLE EULITTORAL *Mytilus californianus* *Lottia* *Collisella scabra*
ENDOCLADIA	
EGREGIA/LITHOPHYLLUM *CORALLINA/PHYLLOSPADIX*	LOWER EULITTORAL *Corallina* *Lithothamnium* *Nuttallina* *Strongylocentrotus*
MIXED REDS/*PHYLLOSPADIX*	
MIXED REDS	

intertidal zonation is Ricketts's own scheme, which we have adopted as a basis for comparison. We use his not because it is inherently better than any other, but because its development was based primarily on observations from the central California coast. A second reason for the adoption of this scheme is that we are most familiar with its strengths and weaknesses.

The generalized scheme of intertidal zonation of rocky shores of Ricketts et al. (1985) is based on the extent of tidal exposure. According to this scheme, there are four well-defined horizontal bands, zones, or associations. The highest, the littorine or splash zone (Zone 1), is most frequently exposed to air. This zone contains mainly bare rock or blue-green algae, but green (*Enteromorpha, Ulva*) or red algae (*Porphyra, Bangia*) and diatoms may be present, especially in the winter or spring (Cubit 1984). The few animals that occupy this zone include the gastropod *Littorina keenae*, the isopod *Ligia* spp., and the limpet *Collisella digitalis*. Zone 2 is the high intertidal and is usually exposed to air for a long period at least once a day. It is characterized by dense populations of barnacles, *Balanus glandula*, and is frequently referred to as the barnacle zone, In addition to barnacles, the algae *Pelvetia fastigiata, Endocladia muricata*, and *Mastocarpus papillatus* (=*Gigartina papillata* in Abbott and Hollenberg 1976) are conspicuous and characteristic members of this zone. The tiny snail *Littorina scutulata/plena*, the turban snail *Tegula funebralis*, and several species of limpets also occupy this zone. Zone 3, often called the mussel zone, is the middle intertidal. It is generally exposed to air for relatively short periods twice a day, and its most conspicuous members are mussels (predominantly *Mytilus californianus* but *M. edulis* may dominate the upper edge of this zone [Suchanek 1978]) and goose barnacles (*Pollicipes polymerus*). Other characteristic species are the predatory snail *Nucella emarginata*, the chitons *Katharina tunicata* and *Nuttallina californica*, and the alga *Iridaea flaccida*. Zone 4 is the low intertidal and is uncovered only by the lowest tides; it may be covered with water most days of each month. This zone typically is easily identified by dense carpets of the surfgrass *Phyllospadix*, upright laminarian algae, and a variety of red algae. Although these plants are the most conspicuous indicators of this zone, it is here that one also finds sponges, hydroids, bryozoans, and ascidians, most of which do not occur higher on the shore.

Many more recent studies of vertical zonation of intertidal organisms along the Pacific coast of North America have turned up a pattern similar to that proposed by Ricketts. In Table 1 we present seven zonation patterns reported from British Columbia to southern California. Species assemblages or zones are indicated in capitals. If a species is capitalized, it typifies or characterizes the assemblage. Within each column the assemblages are grouped vertically in their order of occurrence on the shoreline, without reference to tidal level since the studies are from several different locales with different exposure to surf. The order of species within a group does not necessarily reflect their vertical position in that group. Common to all seven studies are four distinct zones: a high splash or littorine zone (littorines were absent from this zone in Seapy and Littler [1978]), a *Balanus* zone, a mussel zone, and a low *Phyllospadix* zone. Stephenson and Stephenson (1949) did not include a mussel zone, and Seapy and Littler (1978) and Carefoot (1977) show additional assemblages between these common zones. These additional zones could be due to differences in the level of detail of the study, the method used to lump or categorize assemblages, or to actual differences in the community structure of the sites examined. The similarities among the seven sites could be misleading, however, because all the studies in Table 1 were done on massive rocky shores exposed to moderate to severe wave action. The variation in the kinds of shoreline found between British Columbia and Baja California has not been described, and we will address the issue of the way shoreline topography modifies vertical zonation in the sections below.

In addition to the traditional descriptive analyses, zonation has also been studied by assemblage characteristics and mathematical association analyses (Chapman 1974). Den Hartog (1959) characterized zones along the Dutch coast in terms of life form, stratification, successional patterns, and positions in relation to other zones. From his work in central Chile, Santelices (1981) has suggested a zonation based on algal morphologies rather than species. Russell (1972) defined a two-zone shore at a site in the British Isles using cluster analyses on common species, and showed a strong negative correlation between two assemblages. Such correlations remove the subjectivity of traditional descriptions. The general lack of continued work along these lines may indicate a satisfaction with the description of zones and a shift of interest to studies considering the causes of zonation.

One prominent hypothesis regarding the causal agents that produce such distinctive assemblages centers around the concept of critical tidal levels. Critical tidal levels are levels of the shore where some parameter such as time of exposure to air changes abruptly with a small change in tidal height. That zonation patterns are caused by these changes in exposure is intuitively appealing, because limits to distribution of intertidal organisms are also abrupt. Colman (1933), working British shores, and Hewatt (1937) and Doty (1946), working on the Pacific coast of the United States, correlated the vertical distributions of intertidal organisms with critical levels in the tidal cycles associated with abrupt changes in the hours of exposure to air. Shotwell (1950) correlated the upper limits of distribution of *Collisella* with critical tidal levels responsible for extremes in desiccation. The critical tide level hypothesis has been criticized by Connell (1972) largely because the correlation between critical tidal levels and vertical limits of distribution of organisms is not objectively assessed and, looking at the data published by these workers, not very precise. Underwood (1978) refuted the critical tide level hypothesis for British shores on two counts. First, recalculation of the annual emersion times against height on the shore yielded a smooth, monotonic curve without sharp increases in emersion time. Second, boundaries of species' distributions on British shores were found to be randomly distributed, not clumped as would be expected if they were associated with critical tidal levels. In addition, much recent work has shown that biological interactions are also important in controlling the vertical distribution of intertidal organisms, a concept that was not widely acknowledged in the early intertidal literature. Colman (1933) did, however, point out that behavioral responses of gastropods are probably important in explaining their vertical distribution, and that interspecific competition probably explained how extremely distinct boundaries between pairs of algal species could occur without declining abundances of either one near their common borders.

The concept of critical tidal levels has not been entirely discarded, however. Swinbanks (1982) identified several different orders of critical tidal levels that coincided with various cycles of the tide (e.g., daily, monthly, annually), resulting in identification of many more critical tidal levels than proposed earlier by Colman (1933) or Doty (1946). Swinbanks provided examples in which the upper limits of distribution of many intertidal organisms coincided with these critical tidal levels.

In addition to purely physical factors associated with critical tidal levels, it has been shown that biotic factors may also directly affect distributions in the field. Thus, as a *general* hypothesis, critical tide levels has been rejected, although it may apply to a specific distribution in a particular place. The available information now suggests the working hypothesis that a variety of phenomena can affect spatial patterns of distribution. We review this information in the sections that follow.

II. Plants

This section reviews the temporal and spatial patterns of algal distribution, abundance, and reproduction. As will be seen, a synthesis of spatial pattern such as that provided for northern New Zealand kelp communities by Choat and Schiel (1982) or for British shores by Lewis (1964) is impossible for the northeastern Pacific because of the lack of comprehensive, quantitative surveys at numerous sites. Moreover, surveys that are available generally do not consider temporal variation, and do not include a great range of spatial scales. We will use the available information to piece together as complete a picture as possible, and fill in some of the gaps with speculation.

A. Spatial Variation

1. Geographic Distribution

The distribution and abundance of a species on a geographic scale is generally thought to be controlled by general oceanographic conditions and large-scale dispersal, including that by humans (Druehl 1981). Although numerous correlations have been made between the latitudinal distribution of intertidal plants and various environmental factors (e.g., Murray et al. 1980), few of these correlations have been experimentally tested. Moreover, the patterns themselves are often questionable for algae because of incomplete or missing records for particular areas, the difficulty of proving absence, and the use of different taxonomic criteria by different investigators (Druehl 1981).

Given these difficulties, it has been established that the distribution of intertidal seaweeds changes with latitude between British Columbia and Baja California. These changes have been discussed by Scagel (1963) and recently reviewed in detail by Murray et al. (1980) for marine macroalgae in California. Distributional end points for northern and southern species are particularly common along the California coast, producing a rich and diverse flora (Abbott and Hollenberg 1976; Murray et al. 1980). Various biogeographic provinces have been established for the northeastern Pacific (Section III) but, with the exception of the region around Point Conception and perhaps Monterey, changes in the flora with latitude are gradual (Scagel 1963; Murray et al. 1980).

The relatively rapid changes in species composition around Point Conception and Monterey are associated with changes in oceanographic conditions, particularly changes in mean maximum temperature (Murray et al. 1980). The physiological studies of Smith and Berry (1986) suggest that differential tolerance to temperature extremes may affect latitudinal ranges. The observed floral break around Monterey is also correlated with the diversity and extent of rocky habitats in the area, and with the intensity of collection.

These geographic studies are largely based on presence and absence data, and could be used to construct probable intertidal floras for a particular section of coast. In the context of this

TABLE 2. ALGAL SPECIES OR GROUPS OF KNOWN ECOLOGICAL IMPORTANCE THAT VARY IN ABUNDANCE WITH LATITUDE IN CALIFORNIA. Distributions are from Abbott and Hollenberg (1976).

Species	Distribution	Ecological importance	Reference
Red algae			
Algal turfs	More abundant south of Point Conception*	Trap sediment, provide sites for epiphytes, preempt space	Sousa et al. (1981), Stewart 1982
Gigartina canaliculata	Baja California to south Oregon, declining abundance north of Point Conception†	Can exclude other species in boulder fields	Sousa (1979*a*)
Gigartina leptorhynchos	Baja California to Humboldt County, California, declining abundance north of Point Conception†	Can be very abundant south of Point Conception	Sousa (1979*a*)
Rhodoglossum affine	British Columbia to Baja California, but uncommon south of San Luis Obispo County, California	Can form turfs north of Point Conception	M. S. Foster (pers. obs.)
Brown algae			
Hedophyllum sessile	Alaska to Monterey, rare in California	Can displace or provide microhabitat for other species	Dayton (1975)
Lessoniopsis littoralis	Alaska to Monterey	Can displace other species	Dayton (1975)
Postelsia palmaeformis	British Columbia to San Luis Obispo County, California	Can produce primary substratum when dislodged	Dayton (1973), Paine (1979)
Sargassum muticum	Introduced, patchy, British Columbia, San Francisco, Santa Barbara, San Diego, Santa Catalina Island	Can displace at least one other common alga	DeWreede (1983)
Fucus distichus	Washington to Point Conception	Can be very common north of Point Conception, can provide shelter or displace other species	M. S. Foster (pers. obs.)

* Stewart (1982).
† M. S. Foster (pers. obs.).

review, however, one would also like to know whether latitudinal changes in one species cause indirect changes in others. Table 2 lists algal species or groups that vary in abundance with latitude in California, and which are known to affect other species. A number of species or groups are listed, but only the effects of variation in algal turfs have been examined in the context of latitudinal change. Sousa et al. (1981) found that when sea urchins were removed from the low intertidal zone in southern California, red algal turfs developed that could displace juveniles of large brown algae. This is in contrast to similar removals in Washington where turfs do not grow in abundance in the low intertidal zone and where urchin removal results in a persistent cover of large brown algae (Paine and Vadas 1969; Dayton 1975; Paine 1977). Sousa et al. (1981) suggested disturbance as a major cause of these community differences. Many of the algal turf species in southern California are, however, rare or absent to the north (Abbott and Hollenberg 1976; Stewart 1982), and many of the northern large brown algae (e.g., *Hedophyllum sessile*) are rare or absent in southern California (Abbott and Hollenberg 1976). Thus, latitudinal differences associated with sea urchin removal may be simply a result of the natural history characteristics of the species available in an area. Additional experiments in areas where northern and southern species overlap are necessary before the importance of latitudinal variation on local community patterns can be more thoroughly evaluated.

In addition to direct changes in algal species composition, other factors may contribute to the latitudinal variation in the distribution and abundance of algae. Latitudinal changes in grazers may influence local community patterns (Gaines and Lubchenco 1982). Sousa et al. (1981) speculate that large-scale changes in disturbance contribute to local patterns. They suggest that more frequent disturbances by waves and logs in the more exposed intertidal areas north of Point Conception reduce grazer abundance and clear space more frequently, contributing to the maintenance of local stands of large, canopy-forming algae. On the other hand, disturbances associated with shifting sand (Daly and Mathieson 1977; Taylor and Littler 1982) may be more prevalent along the mainland south of Point Conception where sandy beaches are common.

2. VERTICAL ZONATION

The general patterns of intertidal zonation were discussed in the Introduction. Below we examine the causes of algal zonation, and divide these causes in the general categories of physical and biological factors.

a. Effects of Physical Factors

Experimental work on physical factors affecting the vertical distribution of algae on the shore has concentrated on the effects of desiccation in terms of both physiological processes and simple survival. Observations of mortality after intertidal uplifting by earthquakes (Johansen 1972; Bodin and Klinger 1986) and by nuclear bomb testing (Lebednik 1973) dramatically demonstrate the sensitivity of algae to their position on the shore. More classical examples suggesting the importance of desiccation are the raising of zones in areas of high wave exposure and moist air conditions, in areas of drainage from tide pools, and in areas where shade is produced by canopy species or where the substratum faces away from the sun (for review of examples see Lewis 1964; Connell 1972; Carefoot 1977).

Schonbeck and Norton (1978, 1979*a*, *c*) thoroughly investi-

gated the effects of desiccation on some fucoid algae, and found that tissue damage was highly correlated with long exposure during extreme drying conditions. Tolerance to desiccation varied with season and with the position of an alga on the shore (Schonbeck and Norton 1979*c*). Tolerance to dehydration of several intertidal red algae species, as well as individuals of one species (*Porphyra perforata*), is also correlated with tidal height at sites near Monterey (Smith and Berry 1986). Although growth in apical tips of some fucoids increases during short periods of desiccation (Stromgren 1977), it is generally accepted that abiotic environmental conditions become less favorable to algae as intertidal height increases (Foster 1982), and that the upper limits of intertidal plants are set by desiccation (Connell 1972, 1975; but see qualifications below). Descriptive work by Druehl (1967*a*) in a British Columbia inlet suggests that intolerance to high temperatures and low salinity may lower the upper limits of some low intertidal algae.

Transplanting algae vertically on the shore, as done by Schonbeck and Norton (1978), Hodgson (1981), and Foster (1982), is a powerful method of determining the distributional limits of an alga. Such experiments have also indicated that desiccation generally sets upper limits. However, the results of transplanting adults may be ecologically meaningless at a particular site if the juveniles never reach or cannot grow in the area of transplant (Underwood and Denley 1984).

Laboratory studies have suggested that some algae are physiologically best adapted to their position on the shore. Quadir et al. (1979) found that *Fucus distichus*, a representative upper intertidal alga, had maximum net photosynthesis when 20% desiccated. In contrast, Quadir et al. (1979) and Hodgson (1981) found that lower intertidal species such as *Iridaea cordata* and *Gastroclonium coulteri* always had higher net photosynthesis when submerged than when emerged. Schonbeck and Norton (1979*b*) found that increasing nutrient concentrations could compensate for slow growth under conditions of only occasional, brief submergence. Foster (1982) discussed the difficulties of extrapolating the results of physiological studies in the laboratory to actual distributions in the field. In particular, field studies have generally falsified the hypothesis that the lower limits of intertidal algal distribution are determined by physical/chemical factors.

b. Effects of Biological Factors

In addition to physiological attributes of the plants themselves, the biological factors that have been identified as important to the vertical distribution of intertidal algae are competition, grazing, and mutualism. Grazing and mutualism have been shown to directly affect the upper and, in one case, lower limits of intertidal algae. Competition has been shown to affect only the lower limits.

Robles and Cubit (1981) showed that algal growth could be limited by grazing dipteran larvae in an upper rocky intertidal community. After removing larvae by hand and using insecticides with appropriate controls, microalgae and small foliose algae were able to grow at higher levels than previously observed. Careful observation reveals that insects and amphipods are prominent throughout the intertidal zone in central and northern California (Glynn 1965; Robles 1982). As more techniques are developed to manipulate these organisms in field experiments, their potentially important effects on algal distribution may be more thoroughly elucidated.

Molluscan grazers have been manipulated to determine their effect on algal distribution. Castenholz (1961) found that littorine snails could set the upper limit for intertidal diatom mats during the summer season in southern Oregon, and limpets in this same locale can nearly eliminate ephemeral algae (e.g., *Bangia, Porphyra, Ulva*) in the summer (Cubit 1984). Hay (1979) removed intertidal limpets at sites in New Zealand and found that a low intertidal kelp was able to colonize 1.6 m higher than with limpets present. In a similar experiment, but where conditions were drier, colonization did not extend upward. Raffaelli (1979) found little or no effect after removing grazers from the mid-intertidal in New Zealand, but Underwood (1980) suggested that the removal techniques may have been insufficient.

In an exemplary study of grazing effect on mid-intertidal algae using well-designed experiments and considering alternative hypotheses, Underwood (1980) found that foliose algae were able to colonize in areas of grazer removal, but grew to maturity only in unnaturally shaded areas. He concluded that grazing prevents the establishment of algae in the high intertidal but, in the absence of grazers, physical factors control their abundance. In a more recent study, Underwood and Jernakoff (1984) examined the effects of tidal height, wave exposure, and seasonality as well as grazing. Algae again were found to grow best when desiccation was reduced, and no plants became established in the high intertidal if grazers were present.

Thus it seems that the upper limits of algae can be set by grazers. However, the above studies were done in areas inhabited almost exclusively by ephemeral algae (e.g., *Ulva, Porphyra*, and diatoms). Processes may be different for long-lived species. Other factors that should be considered in evaluating the effects of molluscan grazers are their densities, ability to feed effectively under all environmental conditions (e.g., high wave shock conditions), and method of feeding. Scanning electron microscope observations indicate that some species graze rock very thoroughly, while others only crop thalli, having no measurable impact on rates of colonization (Underwood and Jernakoff 1981).

Much less work has been done on the molluscan grazer–algal interactions in the lower intertidal. Dixon (1978) and Sousa (1979*a*, 1984) found that limpet densities decline as algae invade and take over space. Limpets were not able to survive in lower intertidal sites in Australia because algae generally grew fast, covering the substratum so that these animals could not attach (Underwood and Jernakoff 1981). Lubchenco (1980) and Foster (1982) showed that grazing by molluscs can retard but not prevent the establishment of macroalgae at their lower limits of distribution. Moreno and Jaramillo (1983) indicated that the *Iridaea* zone in Chile extended downward if grazers were removed. This manipulative experiment is interesting because it is the first to find that the lower intertidal limits of algae can be set by grazers. Unfortunately, the experiment was pseudoreplicated (Hurlbert 1984) and the measurement of zone width did not indicate direction of zone expansion. These and a variety of other observations (reviewed by Lubchenco and Gaines 1981) indicate that plant–herbivore interactions can be very complex, leading to a variety of patterns at different spatial scales.

Competition with other plants can have significant effects on their lower distributional limits. By removing plants from lower intertidal zones (Hruby 1976), making partial clearings, per-

forming transplant experiments, or a combination of the above (Hodgson 1980; Lubchenco 1980; Schonbeck and Norton 1980; Foster 1982), interspecific competition has been shown to set the lower limits of some macroalgae. In contrast, Dayton (1975) has shown that overstory algae may modify the environment such that other plants may extend their range upward beneath overstory algal canopies (mutualism). Competition may include direct interference (whiplash) or exploitation of light, space, or nutrients. These factors have not yet been separated and tested in the field. Lubchenco (1980) and Foster (1982) found that the basal portions of thalli that remain after the removal of the upright parts of potential competitors still prevented a downward extension of higher intertidal algae, suggesting that inhibition (preemption of space on the substratum) alone can prevent colonization.

Thus, we find that Connell's (1972) generalization that physical factors are important in setting the upper limits, while biological relationships are more important for setting lower limits of organisms in rocky intertidal systems, should be modified. Several studies have indicated that the upper limits of ephemeral algae are set by grazing, a biological interaction. Underwood and Denley (1984) provided a series of alternative hypotheses, mainly dealing with faunal planktonic stages and settlement, that may also modify Connell's generalization. They also pointed out the importance of developing generalizations, but emphasized that these should be critically tested.

3. Variation within Zones

At a specific latitude and within one zonal assemblage, species abundance and distribution can be quite variable. This spatial variation may occur on scales from meters to millimeters, and is caused by physical and biological factors or a combination of both.

Disturbances create new space for colonization, resulting in patches at different stages of succession within an assemblage (Sousa 1979*b*, 1984; Paine and Levin 1981; Section IV). Colonization within a cleared area may be affected by spore availability; limited spore production or short dispersal distances can cause variability between patches (Dayton 1973; Sousa 1984). The timing of a disturbance can also determine the composition of the algal community in the disturbed area (Emerson and Zedler 1978). The coincidence of harsh insolation with low tides also causes localized changes within assemblages. Loss of pigments in algae during such times is commonly observed, and Schonbeck and Norton (1978) noted changes at the upper limits of fucoid zones due to such weather conditions.

At a larger scale, water motion affects species composition. This is commonly noted when comparing the species composition of exposed and sheltered rocky shores (e.g., Ricketts et al. 1985). The most obvious possible cause of the differences is ability of adults to withstand wave forces, but this does not explain why plants characteristic of exposed sites are generally not found in quiet water. Druehl (1967*b*) found that around Vancouver Island, the long form of *Laminaria groenlandica* is found in areas of heavy surf, the short form in areas of moderate surf, and *L. saccharina* is only found in calm areas. Experiments indicated this was due to different abilities to withstand water motion and the ability of *L. saccharina* to grow and reproduce in the reduced salinities associated with the calm water sites. Dayton (1975) noted that recovery rates of *Hedophyllum sessile* in partial clearings were much more rapid at exposed sites. More complex interactions may also affect species composition along exposure gradients. Paine (1979) proposed that moderate wave intensity creates space in mussel beds, and that this was necessary for the local persistence of *Postelsia palmaeformis*. Lubchenco and Menge (1978) discussed other factors that have variable importance along a gradient of wave exposure in New England. For instance, the abundance of grazers (littorines) was lower at exposed sites, allowing for a greater abundance of ephemeral algae, which in turn compete with *Chondrus crispus*. Thus, a series of interactions slows the succession rate in exposed areas. Additional mechanisms affecting spatial variation along exposure gradients are discussed in Section III.A.4.

Tide pools also cause species variation within an assemblage. Underwood and Jernakoff (1984) found that during dry seasons, foliose algal growth increased in artificially made tide pools but declined on adjacent rock platforms. Lubchenco and Gaines (1981) reported different herbivore taxa in pools than outside, and Lubchenco (1982) found that fucoids can be excluded from protected pools by the joint action of herbivores and algal competitors. However, in areas with a high frequency of physical disturbance, Dethier (1984) contended that herbivory, competition, and predation were less important than physical factors in structuring tide pool communities.

Substratum composition and relief can create different microhabitats. *Fucus* growing on barnacles are more easily detached than when growing on rock (Barnes and Topinka 1969), plant loss during storms is higher on unstable substrata (Gunnill 1985), and algal zones are raised to much higher levels on limestone than on basalt (Den Hartog 1959). Harlin and Lindbergh (1977) determined that surface relief can regulate the development of an algal community. Using settling plates made of acrylic discs with layers of different diameter particles, they found that macroalgae generally colonized areas with greater surface relief. Greater relief may provide refuges from grazing (see below) and help prevent desiccation (Jernakoff 1983). Areas influenced by sand movement and burial often have floras composed of perennial species that can tolerate such disturbance, and ephemeral species that invade when sand is not present (Daly and Mathieson 1977; Taylor and Littler 1982). D'Antonio (1986) suggested that the perennial red alga *Rhodomela larix* is also abundant in such areas because sand provides a refuge from competitors, grazers, and epiphytes.

Algal patchiness can also be caused by localized size or spatial refuges from grazing. Lubchenco (1983) found that grazing gastropods prevented the establishment of *Fucus* on smooth rock, but only very high snail densities could prevent establishment of this plant in areas where crevices and barnacles were present. A similar interaction occurs between littorines and *Enteromorpha* (Petraitis 1983). Jernakoff (1983) suggested that the patchy distribution of algae within the barnacle zone reflects areas where spores have escaped grazing in the past. He indicated this is an escape by chance, because grazers were found to be effective in all microhabitats. Algae may find refuge from grazing by growing on the shells of herbivores. Where surrounding rock surfaces are barren of macroalgae, *Ulva* and *Enteromorpha* can be found growing on limpets (e.g., *Notoacmea scutum*, Ricketts et al. 1985) and chitons (W. P. Sousa, pers. comm.), and perennial algae are found on some black abalone in the Monterey Bay

area and on San Nicolas Island (A. P. De Vogelaere, pers. obs.). Gaines (1985) found that local patchiness in *Iridaea cordata* was related to the distribution of the grazers *Katharina tunicata* and *Strongylocentrotus purpuratus*. At his study sites in Oregon, *I. cordata* abundance was greatly reduced on horizontal surfaces where these grazers were most abundant. When the grazers were experimentally reduced, the alga's distribution became more uniform. Grazers can also create patchiness by accelerating succession (Lubchenco and Menge 1978; Sousa 1979*a*) and, in the case of the territorial limpet *Lottia gigantea*, grazing creates large patches free of upright organisms (Stimpson 1970), while limpet mucus locally enhances diatom growth (Connor and Quinn 1984).

Grazing may also generally alter algal abundance and species composition. B. A. Anderson (pers. comm.) noted that mites can graze patches in stands of the high intertidal green alga *Prasiola meridionalis*. Duggins and Dethier (1985) removed the chiton *Katharina tunicata* from a low intertidal site in Washington that was dominated by the kelp *Hedophyllum sessile* and considerable bare space. Algal abundance and diversity rapidly increased after removal, resulting in a low intertidal kelp bed. In the continued absence of grazing, patchiness in this new assemblage was maintained by physical disturbance.

Disease caused by a variety of pathogens has frequently been noted in intertidal algae (Andrews 1976, 1977; Goff and Glasgow 1980), but little is known about the effects of disease on natural populations (Andrews 1977). Smith and Berry (1986) found that the incidence of an endophytic brown alga and fungal pathogens in the blades of *Porphyra perforata* increased as tidal height decreased. They suggested that such infections may prevent *P. perforata* from living in low intertidal and subtidal habitats. A fungus alters the morphology of *Blidingia minima* (Abbott and Hollenberg 1976), and we have noted large (~15–20 cm in diam.) black patches in stands of this species presumably caused by fungal infection.

Epiphytes can be common on intertidal algae but, like pathogens, their effects on host populations remain generally uninvestigated. Epiphytes are commonly associated with senescent plants (M. S. Foster, pers. obs.). In such circumstances their effects on the growth and survivorship of the host may be minor. Sousa (1979*a*) suggested that epiphytes may increase the mortality of middle successional species (e.g., *Gigartina leptorhynchus, Rhodoglossum affine, Gelidium coulteri*) at sites near Santa Barbara, enhancing conditions for later dominance of *Gigartina canaliculata*. D'Antonio (1985) found that epiphytes on the red alga *Rhodomela larix* at sites in Oregon and Washington can decrease growth and reproductive output, and increase axis breakage. Laboratory studies suggested that herbivorous amphipods may reduce these effects by removing epiphytes.

Finally, certain species provide microhabitats for other organisms. Obligate understory algae are considered an ecological category of algae by Dayton (1975). They die when the overstory canopy species are removed. Death is caused either from desiccation, exposure to excessive light intensity, or from physical battering. These "obligate" understory algae are often intertidal representatives of otherwise subtidal species that extend their distribution upward only when physically protected. Numerous animals are also associated with particular plants (Glynn 1965; Borden et al. 1975; Hill 1980; Gunnill 1983; Section III).

In summary, algal variability within zones at the microhabitat scale can be caused by physical disturbances, dispersal limitations, pools, substratum types and relief, grazing, interactions between grazers and substratum type, and particular associations, especially between understory algae and the overstory of larger perennial algae.

B. Temporal Variation

1. Within Years

As pointed out in the Introduction, early work on intertidal ecology was primarily concerned with the description of vertical patterns of distribution, while more recent work has focused on factors affecting these and other spatial patterns. Very few studies have examined temporal variation. Natural history observations suggest that temporal variation in species abundance and composition is lower than spatial variation (i.e., differences between intertidal zones are more apparent than differences between seasons within a zone), as do data from control quadrats used in various experimental studies in the northeastern Pacific (British Columbia and Washington: Dayton 1975; DeWreede 1983; Oregon: Turner 1983*a, b*; central California: Abbott 1980; Foster 1982; southern California: Emerson and Zedler 1978; Littler 1980; Stewart 1982). Neither Ricketts et al. (1985) nor Carefoot (1977) have sections on temporal variability, and it is not discussed in the review by Lewis (1964) of British shores, or by Stephenson and Stephenson (1972) in their review of the shores of the world. Based on his multi-site seasonal surveys in southern California, Littler (1980: 295) concluded that "local or even site-specific conditions tended to predominate more often and obscured any broad climatic effects (overall seasonal patterns)." In contrast, Sousa (1979*a*) noted considerable seasonal variation in algal abundance and recruitment at sites near Santa Barbara.

One might expect temporal variability in the northeastern Pacific to be low because the more common intertidal algae are perennial and perhaps long lived. As discussed by Connell and Sousa (1983), however, if variability were scaled to lifespan, these plants may vary as much as annuals. Thus, stability remains a question until ages are known and demographic studies are done over the appropriate time scales. There are few published observations showing that seasonal differences in the abundance of these species are related to individual mortality. However, some of these perennials vary in the abundance of vegetative parts. *Hedophyllum sessile*, a large brown alga that can be abundant in areas of moderate wave exposure, may drop from 100% cover in summer to 50% in winter due to defoliation (Dayton 1975). The red algae *Iridaea cordata* and *I. flaccida* have perennial holdfasts and generally annual blades. Blades begin to grow in late winter, reach their maximum size in midsummer, and then reproduce and senesce in the fall (Hansen and Doyle 1976; Hansen 1977; Foster 1982). Long-term records of *I. flaccida* abundance at a site near San Luis Obispo clearly show this regular cycle (Fig. 1). Hansen (1977) suggested that light may limit growth of *I. cordata* in winter and that maturation is genetically controlled. Emerson and Zedler (1978) found that the perennial articulated coralline *Lithothrix aspergillum* declined in cover during the summer at a site near San Diego as a result of increased temperatures and desiccation during low tides. Sousa (1979*a*) noted extensive winter defoliation at sites near Santa Barbara when warm winds coincided with low tides.

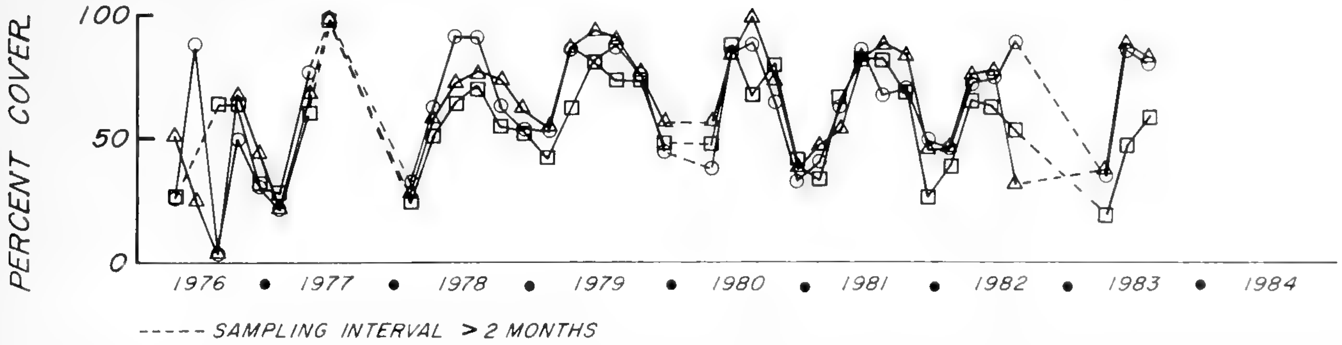


FIGURE 1. *Iridaea flaccida* abundance at +3 ft above MLLW near San Luis Obispo, California. Data from three fixed 0.25-m² quadrats at one site. Quadrats sampled by noting cover under 60 randomly placed points (from PGE 1984).

Occasional widespread loss of the blades of perennial species occurs in Monterey when hot weather (no fog) coincides with summer low tides (M. S. Foster, pers. obs.).

The general lack of reported seasonal changes may to some extent reflect the gross level of sampling (visual estimates of cover, bias towards large, canopy species) and the relatively short duration of most studies. In those studies that have used more detailed sampling over longer periods, or that have followed individual or cohorts of plants, within-year changes in abundance are usually found. In a particularly thorough study of reproduction, recruitment, and standing stocks of one green (*Codium fragile*) and five brown (*Eisenia arborea, Egregia laevigata* [=*E. menziesii* in Abbott and Hollenberg 1976], *Sargassum muticum, Halidrys dioica,* and *Cystoseira osmundacea*) algae, Gunnill (1980*a*) found clear seasonal variation in numbers of individuals in almost all species in his study sites near San Diego. Variation was largely due to variation in recruitment. Recruitment was most common in spring–summer, and appeared related to changes in reproduction. Similar trends were identified for the brown alga *Pelvetia fastigiata* (Gunnill 1980*b*). Gunnill (1980*a*) concluded that these population fluctuations were related to a complex of environmental factors including cloud cover, temperature, and wave action. Stewart (1983) showed distinct seasonal patterns of abundance in several algal turf species correlated with seasonal changes in sand accumulation.

Probably the longest, most thorough observations of intertidal plants and animals come from monitoring programs done by companies with coastal power plants in California. Environmental monitoring around the Diablo Canyon nuclear power plant near San Luis Obispo has revealed seasonal patterns in almost every species examined (PGE 1984). In addition to *Iridaea flaccida* (Fig. 1), the perennial red algae *Endocladia muricata, Gigartina canaliculata,* and *Mastocarpus papillatus* all change abundance seasonally, usually with maximum cover in summer and early fall and minimum cover in winter and early spring (Fig. 2). Much of this change appears related to a cycle of winter storm damage followed by new growth (PGE 1984), but seasonal variation in recruitment could also be important (Gunnill 1980*a, b*). We stress again that Figures 1 and 2 represent changes in cover. How much of this variation is due to individual death and recruitment is unknown.

Annual species or relatively large, annual stages in the life histories of heteromorphic plants do often undergo distinct seasonal changes in abundance (Mumford 1975; Lubchenco and Cubit 1980; Cubit 1984). *Porphyra* spp., *Bangia fuscopurpurea,* and *Urospora penicilliformis* are particularly common in winter and spring in Oregon, growing on established plants and animals or bare space (Lubchenco and Cubit 1980; Cubit 1984). Related plants, including some brown algae, go through similar cycles in the northeastern United States (Lubchenco and Cubit 1980), and in southeastern Australia (Underwood and Jernakoff 1984). In both areas in the United States, the winter algal blooms appear related to more favorable abiotic conditions for the algae that allow their growth to exceed the ability of grazers to remove them (Castenholz 1961; Lubchenco and Cubit 1980; Cubit 1984). Similarly, Underwood and Jernakoff (1984) found that a reduction in grazing further increased algal cover in winter. This temporal escape from grazing by growth is analogous to the spatial escape suggested for algae in the low intertidal zone (Underwood and Jernakoff 1981; Foster 1982).

As demonstrated by Gunnill (1980*a, b*), some of the seasonal variation in abundance is a consequence of seasonal variation in reproduction. However, recruitment is not necessarily correlated with peaks in reproduction. For example, *Iridaea* sp. at a site near Monterey was recruited in high densities in quadrats cleared in fall and spring, while spore production was highest in late summer and fall (Foster 1982). As indicated in Table 3, of those algae in the northeastern Pacific for which there are data on reproduction, most have a seasonal reproductive period or are continually reproductive but show seasonal reproductive peaks. Peak reproductive periods occur at various times for various species, but reproduction seems to be most common in fall, and to a lesser extent in summer and winter. However, there is little information available that relates reproduction to adult abundance patterns (but see Gunnill 1980*a, b*; Foster 1982). This is not a simple task because the presence of reproductive structures does not necessarily mean spores are being released. Moreover, as suggested by Gunnill (1980*a*), variation in adult abundance in the absence of grazers results from a complex interaction of reproduction, availability of space for recruitment, and proper environmental conditions for growth. A demographic approach to seasonality in perennial intertidal algae is clearly necessary to unravel this complexity. In contrast to most animals, perennial algae appear to have very reduced planktonic stages (Dayton 1973; Sousa 1984) and thus a more complete understanding of plant population dynamics may be easier to achieve.

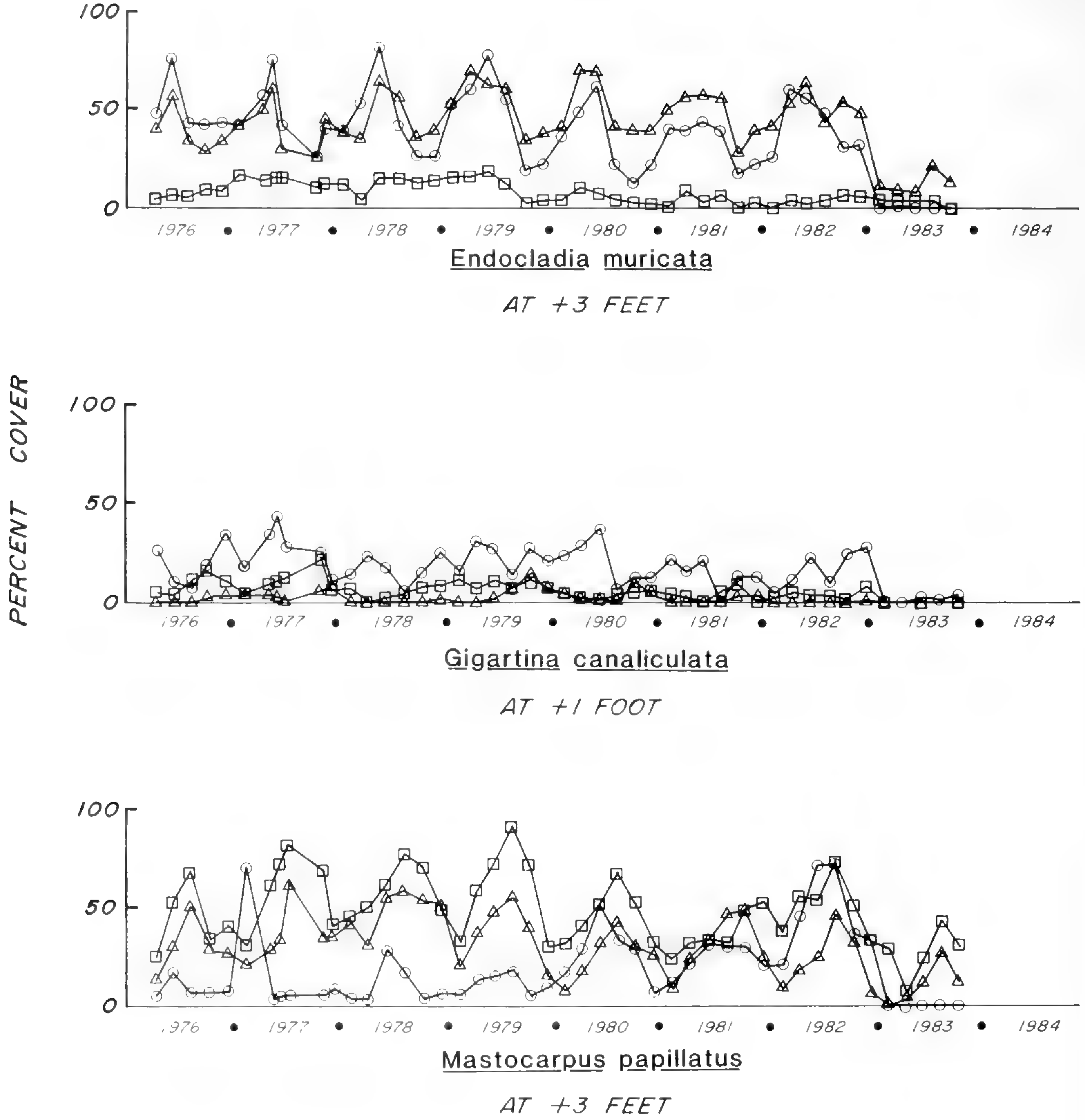


FIGURE 2. Year-to-year variation in three perennial algae near San Luis Obispo, California. (For details, see legend, Fig. 1; three fixed quadrats used at each tidal height.)

2. Between Years

Most of the difficulties mentioned above in assessing seasonal patterns are even more applicable to between-year patterns. Long-term temporal changes associated with various kinds of pollution (e.g., Widdowson 1971; Harris 1983; Section V) and the introduction of exotic species (DeWreede 1983) have been documented. However, there are few reports of "natural" long-term temporal change, and the 1976–83 time series near San Luis Obispo suggests little change at this site (Fig. 1, 2). The declines in the abundance of most species in 1983 were associated with extreme 1982–83 winter storms. Gunnill (1980*a*, *b*), however, found considerable year-to-year variation in recruitment for most species he studied in southern California. This variation in recruitment was often site specific, as was the variation in cover at the sites near San Luis Obispo (PGE 1984). Gunnill (1985) also found that mortality of low intertidal kelps increased at a southern California site during the most recent

El Niño warm water period, and the polychaete *Phragmatopoma californica* increased in abundance following this El Niño, replacing much of the intertidal algal cover in some areas near Santa Barbara (W. P. Sousa, pers. comm.). In contrast, Paine (1986) could not detect any effects of this oceanographic event on an intertidal community in Washington, even though there were changes in the properties of the offshore water.

When adequate sampling methods are used over long periods of time, temporal variation in intertidal algal abundance is clearly evident (PGE 1984). The innovative study by Dungan (1986) indicates that temporal variability in algal populations can be caused by a complex of interacting direct and indirect factors. Temporal variability is generally more subtle and difficult to describe than changes in space (e.g., zonation), and we have only begun to describe this variation and the factors responsible for it.

TABLE 3. TIME OF SPORE OR GAMETE PRODUCTION FOR ALGAL SPECIES IN THE NORTHEASTERN PACIFIC.

Species	Time of reproduction	Reference
Red algae		
Gigartina canaliculata	All year with summer–fall peak	Abbott (1980)
Gigartina leptorhynchos	All year with summer–fall peak	Abbott (1980)
Mastocarpus papillatus	All year with winter peak	Northcraft (1948)
Iridaea cordata	All year with summer–fall peak	Hansen and Doyle (1976)
Iridaea flaccida	All year with winter peak	Northcraft (1948)
	All year with summer–fall peak	Foster (1982)
Rhodoglossum affine	All year with winter peak	Northcraft (1948)
Rhodomela larix	All year with spring–summer peak	DeWreede (1983)
Brown algae		
Cystoseira osmundacea	Fall–winter but variable	Gunnill (1980*a*)
Eisenia arborea	Late fall–spring	Gunnill (1980*a*)
Egregia laevigata	Late fall–spring	Black (1974), Gunnill (1980*a*)
Halidrys dioica	Spring–summer	Gunnill (1980*a*)
Hedophyllum sessile	Early winter	Widdowson (1965)
Pelvetia fastigiata	Winter–spring	Gunnill (1980*b*)
Postelsia palmaeformis	Spring–fall	Dayton (1973), Paine (1979)
Sargassum muticum	Late spring–early summer	Gunnill (1980*a*)
Green algae		
Codium fragile	Winter–spring	Gunnill (1980*a*)

III. ANIMALS

This section is organized in a manner similar to Section II. We will first review overall latitudinal and microhabitat distributional patterns and how they vary (vertical zonation was discussed in the Introduction). Then we will treat current knowledge of both within-year and between-year variation of these patterns. Our concern is mainly with macroscopic sessile, sedentary, or slow-moving animals that can be noted easily and studied during low tides, primarily because these are the animals most commonly studied. There have been virtually no studies of microscopic benthic organisms in the rocky intertidal, even though such organisms must be abundant and important in the system. For example, in his detailed study of the *Endocladia–Balanus glandula* association, Glynn (1965) found that blue-green algae, diatoms, microscopic green algae, small oligochaetes, crustaceans, tardigrades, and mites were abundant. The copepod *Tigriopus californicus* can be extremely abundant in tidepools above mean high water (Dethier 1980), but few ecological studies have been done on it (Cooper 1977; Dethier 1980). Indeed, most marine macroscopic animals pass through a juvenile stage that places them within the meiofauna, and their survival there is crucial if they are to become adults (Thorson 1966; Highsmith 1982; Watzin 1983). We also will not review the effect of parasites and diseases on the distribution and abundance of host organisms, even though such effect may be substantial (e.g., Williams and Ellis 1975; Curtis and Hurd 1983; Curtis 1985), for as Ricketts et al. (1985) pointed out (p. 460) ". . . too few studies have been done on intertidal organisms to comment with much certainty about the specific effects [of parasites and diseases] on abundance and distribution." Moreover, we will not treat "visitors" to the intertidal zone, such as birds and mammals during low tides, and fishes during high tides, even though predation and other forms of disturbance by these animals may be of paramount importance to the more permanent residents (e.g., Boal 1980; Castilla 1981; Frank 1982; Moreno et al. 1984; Warheit et al. 1984; Branch 1985; Lindberg et al. in press).

A. Spatial Variation

1. GEOGRAPHIC DISTRIBUTION

The coastline from British Columbia to Baja California includes three of the four major faunal zones: cold-temperate, warm-temperate, and tropical. Several faunal provinces have been suggested in this area, the precise number depending upon the investigator. The boundaries between the provinces are based upon distributional patterns of several major taxonomic groups and their precise locations are still a matter of debate and research. Over a dozen different schemes for dividing the west coast of North America into faunal provinces have been proposed over the past 120 years and the scheme one employs is mostly a matter of personal choice. Hall (1964), Valentine (1966), and Briggs (1974) each reviewed previous schemes of faunal provinces and each proposed their own. Recognizing that there are points of contention in all biogeographic schemes, the one that we use in this review (Fig. 3) is based on that of Briggs (1974). Under this scheme, the coast between southeast Alaska and Baja California includes three zoogeographic provinces that reflect the three major faunal zones. The Oregonian Province extends from Dixon Entrance in southeast Alaska to Point Conception in California. The San Diego Province extends south from Point Conception to Magdalena Bay on the Pacific side of the Baja Peninsula. The tip of the Baja Peninsula south of Magdalena Bay is a spatially isolated portion of the Mexican province, which extends south to Tangola-Tangola Bay, in southern Mexico.

Generally, provincial boundaries are established by examining the distributions of specific animal groups. Echinoderms, nemerteans, ascidians, hydroids, bryozoans, fishes, and mol-

FIGURE 3 Zoogeographical provinces of the Pacific coast of North America (modified from Briggs 1974).

luscs have all been used as the basis for establishing biogeographic regions. Areas that include the termini of many species ranges are considered as faunal boundaries. Areas where there is a high degree of endemism—that is, areas characterized by species that occur only in that area and nowhere else—are considered faunal provinces. The precise locations of provincial boundaries remain topics of debate and research because it is difficult to establish objective, nonarbitrary criteria for defining them. How much endemism is required for an area to qualify as a province, or how many range termini must occur in a region for it to be considered a boundary? Valentine (1966), Hayden and Dolan (1976), and Seapy and Littler (1980) utilized computer assisted techniques such as cluster analysis to provide more objective criteria in describing faunal provinces. It is encouraging that, in general, their proposed biogeographic schemes agree with those of previous workers.

Species populations within faunal provinces are not uniformly distributed but often exhibit large-scale spatial variation. Seapy and Littler (1980) suggested that due to current flow patterns and eddies, some islands in the San Diego Province (which they called the California Province) are populated with animals characteristic of the Oregonian Province while others are populated by species characteristic of the San Diego Province. Kanter (1980) found that the species composition of mussel communities was highly variable throughout the Southern California Bight, and that patterns of similarity among mussel communities at different geographical locations were related to patterns of planktonic larval dispersal by prevailing currents.

What are the underlying factors responsible for biogeographic patterns? Temperature is the most often cited causal agent (Hutchins 1947, for example), but a direct correlation between faunal distributions and temperature has not yet been shown. Valentine (1966) attributed this difficulty to the fact that no single criterion for a "temperature factor" can be found, and concluded that overall, provincial and subprovincial patterns are controlled by thermal regimes but not everywhere by the same thermal attribute. Fritchman (1962), summarizing his extensive study of reproductive cycles of limpets in central California, concluded that the ranges of the limpets studied are determined by failure of reproduction at unsuitable temperatures, and these temperatures are different for different species. Death of adults is probably not involved. Similarly, Hall (1964) suggested that the number of consecutive days or months that shallow sea temperature is appropriate for reproduction and early growth may be the critical factor limiting molluscan distributions. Hayden and Dolan (1976) defined marine climate boundaries based on the distribution of water masses and current flow within the masses which integrate temperature, salinity, and large-scale advection of waters, and found that provincial boundaries agreed well with the distribution of these marine climates. Mokyevsky (1960) suggested that latitudinal variation in species distributions was related not only to temperature but also to moistening of intertidal organisms, which is influenced by tidal range, surf conditions, and seasonal and sporadic changes in sea level. Wethey (1985) argued that, at high latitudes, the geographic distribution of mid- and low-intertidal species that are large, long-lived, and slow to reproduce is related to catastrophic mortalities caused by sea ice.

The provincial boundaries shown in Figure 3 coincide with positions of changes in the flow of major current systems. The northern boundary of the Oregonian Province at Dixon Entrance coincides with a transitional area where the eastward-flowing West Wind Drift splits into a northward-flowing current and the southward-flowing California Current (Briggs 1974). The boundary between the Oregonian and San Diego Provinces at Point Conception is well-defined and coincides with the departure of the California Current from the coastline. The California Current continues its southerly flow while the coastline veers eastward south of Point Conception. The southern California coastline and inner Southern California Islands are bathed by the warm, northwesterly-flowing Southern California Eddy (Seapy and Littler 1980). Point Conception thus represents a point of abrupt change in water temperature. The temperate/tropical boundary between the San Diego and Mexican Provinces probably arises from the declining influence of the California Current as it turns westward away from the coastline just south of the boundary. Some workers have suggested the presence of a distribution boundary at Monterey Bay, central California (Hall 1964; Valentine 1966; Hayden and Dolan 1976) but Hartman and Zahary (1983) found no evidence supporting this view. It may be, as we also suggest for algae (Section II), that such a boundary is an artifact of habitat diversity and intense sampling in this region.

The coastline from Alaska to southern California is thus inhabited by species that have arctic, cold- and warm-temperate, and tropical affinities. Although each province has characteristic assemblages of species, provincial boundaries are not distinct and considerable species overlap occurs, even across such well-defined boundaries as Point Conception. Also, the degree of overlap changes with time. Many species of warm-water fishes are known to find their way as far north as Monterey Bay during periods of extreme warm water, such as the 1982–83 El Niño. If such anomalies are sufficiently long-lasting, overlap will show up in the invertebrate fauna as well, as illustrated by the increase in *Aplysia californica* abundance in San Francisco Bay during the 1982–83 El Niño (W. P. Sousa, pers. comm.).

TABLE 4. LATITUDINAL DISTRIBUTION OF EIGHT SPECIES WHICH CAN BE IMPORTANT OCCUPIERS OF PRIMARY SPACE IN ROCKY INTERTIDAL COMMUNITIES. Distributional data are from Morris et al. (1980).

Species	Northern boundary	Southern boundary
Anthopleura elegantissima	Alaska	Baja California
Phragmatopoma californica	Central California	Ensenada (Baja California)
Balanus glandula	Aleutian Islands	Bahia de San Quintin (Baja California)
Chthamalus dalli	Alaska	San Diego, California
Chthamalus fissus	San Francisco	Baja California
Semibalanus cariosus	Bering Sea	Morro Bay, California
Tetraclita rubescens	San Francisco	Cabo San Lucas (Baja California)
Pollicipes polymerus	Alaska*	Punta Abreojos (Baja California)

* Newman and Killingley (1985).

To our knowledge, the extent to which latitudinal variation in the distribution of intertidal organisms contributes to variation in other organisms has not been examined. Several species that are potentially important space occupiers in rocky intertidal communities have distributional boundaries within the geographic area considered in this review (Table 4). The polychaete *Phragmatopoma californica* inhibits both anemones (*Anthopleura elegantissima*) and macroalgae in the low intertidal zone in southern California (Taylor and Littler 1982). Likewise, *Tetraclita rubescens* can be abundant in the mussel zone and may influence the distribution and abundance of mussels and the many species associated with them. *Chthamalus fissus* and *Chthamalus dalli* occupy identical microhabitats in the intertidal zone; *C. dalli* occurs from Alaska to San Diego but *C. fissus* occurs only from San Francisco to Baja California. It would be very difficult, however, to attribute any differences in the structure of rocky intertidal habitats between northern and central California to the northern range limit of *C. fissus*.

2. VERTICAL ZONATION

In the Introduction we briefly described the patterns of vertical zonation on the west coast of North America. Here we discuss mechanisms that contribute to these patterns in animal distribution.

a. Causes of Zonation

Connell (1972) suggested the generalization that upper limits of sessile animals tend to be set by physiological tolerance to physical parameters such as desiccation, temperature, and salinity, and lower limits tend to be set by biological interactions such as competition and predation. In addition, the vertical distribution of motile animals may be regulated by behavioral mechanisms, which will be covered later in this section.

The most commonly reported factor responsible for setting the upper limits of intertidal animals is desiccation (Broekhuysen 1940; Shotwell 1950; Connell 1961*a, b*; Kensler 1967; Foster 1971*a, b*; Wolcott 1973; Dixon 1978; Peterson 1979). This is usually based on the correlation between the ability of an organism to withstand desiccation stress (often determined in the laboratory) and the position of its upper limit in the intertidal zone, but there are obvious problems with assuming cause and effect from such correlation. Wolcott (1973) provided more rigorous criteria for accepting the hypothesis that desiccation was responsible for the upper limit of intertidal limpets, and found that desiccation was responsible for the upper limits of limpets in Zone 1 but not in Zone 2. Compelling evidence for the role of desiccation in setting the upper limits of distribution of sessile organisms comes from chance observations of mass mortality at the upper limit of distribution under unusually dry conditions in the field (Connell 1961*a*; Frank 1965; Foster 1971*b*; Seapy and Littler 1982). Dayton (1971) experimentally tested the hypothesis that desiccation sets distributional limits on the sea anemone *Anthopleura elegantissima* by transplanting animals to areas where they normally do not occur in Puget Sound. Although the animals survived well through the winter, they all (p. 360) ". . . began to turn brown and die from desiccation" after the tides moved to daytime hours in the spring.

Other factors have been implicated in setting upper limits to species distributions. Upper limits of distribution may be set by tolerance to thermal stress independent of desiccation stress, though this has not been frequently reported (Connell 1961*a, b*; Foster 1969, 1971*a*). Frank (1965) found increased mortality in a population of *Colisella digitalis* in Coos Bay, Oregon, during two winter periods with exceptionally severe frosts. The vertical distribution of adults may also be determined by patterns of larval recruitment. Denley and Underwood (1979) studied the zonation patterns in two barnacle species in Australia, and found no settlement of cyprids above the zone of adults. Grosberg (1982) found that the vertical distribution of the late planktonic stages of two barnacle species in central California, *Balanus glandula* and *B. crenatus*, corresponded almost exactly with the vertical distribution of adults on the shore. Similarly, Strathmann and Branscomb (1979) found that although the upper limit for adult *Semibalanus cariosus* is determined by mortality of juveniles from drying or high temperature, and occasionally large numbers of cyprids settle too high, most of the time the cyprids successfully use cues to avoid settling above the zone in which they can survive. Underwood (1972) rejected the idea that physical factors set the upper limit of distribution of four species of trochid gastropods because in the laboratory they were able to withstand far longer periods of emersion than they experienced in their natural habitat on British shores. He suggested that food availability may set the upper limit to their distribution. Salinity may potentially limit the upper distribution of intertidal invertebrates, but studies have generally shown that it is unimportant (Broekhuysen 1940; Bock and Johnson 1967; Foster 1971*b*; Wolcott 1973). In Greenland, however, where seasonal ice formation and subsequent icemelt runoff are dominant physical attributes of intertidal existence, the vertical distribution of *Semibalanus balanoides* is determined by the sensitivity of settling larvae to the salinity of the icemelt (Petersen 1962). Luckens (1970) observed extensive mortality in New Zealand barnacles when heavy rain coincided with low tides.

Finally, biological factors cannot be ruled out as determinants of upper distributional limits. Choat (1977) experimentally demonstrated that interspecific competition between *Collisella digitalis* and *C. paradigitalis* confined the latter species to lower intertidal levels. Dixon (1978) reported that the upper limit of one of four species of intertidal limpets in southern California was determined by exploitative competition for food with species higher on the shore.

The idea that lower limits of distribution are set by biological interactions first gained widespread exposure by the now classic work of Connell (1961*a*). In Scotland, the barnacle *Chthamalus stellatus* occurs higher on the shore than *Semibalanus balanoides*. Connell (1961*a*) found that when the two species came into contact, *S. balanoides* grew faster than *C. stellatus* and killed *C. stellatus* by lateral crushing, smothering, or undercutting. Experimental removal of *S. balanoides* resulted in lowering of the lower distributional limit of *C. stellatus*, providing strong support for the idea that competition with *S. balanoides* set the lower distributional limit of *C. stellatus*. *Chthamalus stellatus* naturally occurs in the lower intertidal zone south of *S. balanoides*'s southern limit. More recent examples of competitive interactions setting lower limits of animal distribution include studies by Menge (1976) and Peterson (1979).

Predation has also been shown to limit the lower distribution of intertidal animals. Perhaps the best known example of this phenomenon is the work of Paine on the outer coast of Washington state. By experimentally removing the predatory sea star *Pisaster ochraceus*, he showed that predation by sea stars upon the mussel *Mytilus californianus* prevented mussels from occupying lower reaches of the intertidal zone (Paine 1966, 1974). Working in the same area, Connell (1970) also showed the importance of predation in setting lower distributional limits of barnacles. On the coast of Washington state, *Balanus glandula* occurs as a distinct narrow horizontal band. Cyprids settle in a wider band than the adults but those in lower areas are consumed by predators (Connell 1970; Dayton 1971; Strathmann and Branscomb 1979). Predation has also been shown by Menge (1976) and Fawcett (1984) to set the lower distributional limits of other intertidal organisms.

The vertical distribution of motile invertebrates may be determined by the same kinds of factors that regulate the distribution of sessile species (Branch and Branch 1981; Creese 1982). In addition, behavioral responses of motile invertebrates can prevent them from encountering physiological stressful conditions above their normal range and predators and competitors below. Frank (1965) reported that the vertical distribution of *Collisella digitalis* in Coos Bay, Oregon, was determine behaviorally, and that movement patterns were related to moisture conditions. Wolcott (1973) found that although desiccation stress appeared to set the upper limit of vertical distribution for limpets in the high intertidal, limpets from lower on the shore possessed behavioral adaptations which prevented upward migration into potentially lethal microhabitats. At Bodega Head, central California, the ability of *Littorina keenae* and *L. scutulata/plena* (see Mastro et al. 1982 for discussion of the taxonomic distinctions between these two sibling species) to withstand desiccation, fresh water, and temperature was correlated with their respective tidal heights (Bock and Johnson 1967). Their upper and lower limits, however, were set by positive and negative geotaxic responses that could be reversed in responses

to cues from the habitat (Bock and Johnson 1967). Haven (1971) indicated that active behavioral choice was the proximate cause of observed distributional patterns in *Collisella scabra* and *C. digitalis* in Pacific Grove, central California. Mitchell (1980) could find no correlation between tolerance to thermal stress, continuous submergence, or rate of water loss and tidal height in six species of New Zealand gastropods, and suggested that behavioral selection for distinct microhabitats explained the vertical separation of these six species. Defensive responses of marine gastropods to sea star predators are well known, and it is possible that they may explain the vertical distribution of some intertidal species. For example, at a site near Monterey, central California, the limpets *Notoacmea scutum* and *Collisella limatula* move upward in the presence of the predator *Pisaster ochraceus* that occurs lower in the intertidal zone (Phillips 1976). Fawcett (1984) found that the lower limit of the distribution of *Tegula funebralis* on the shore is due to the snails' defense behavior. Moreover, behavioral differences in snails in northern versus southern California explained a latitudinal difference in the lower limits in this species' distribution. Thus, behavioral responses elicited by predators, rather than predation per se, can control the lower limit of some gastropods' distributions.

b. Modifications of Vertical Zones

It has long been recognized that zonation patterns are often modified by a variety of factors, the most important of which is exposure to the impact of breaking waves. This factor has been considered by several investigators (Southward 1958; Lewis 1964, 1968; Connell 1972; Seapy and Littler 1978; Tsuchiya 1979; and others), and the central idea is that increased frequency of wave action, increased height of the waves, and raising of the level reached by spray are accompanied by raised boundaries of a majority of littoral species (Lewis 1964, fig. 53; Ricketts et al. 1985, fig. 5). Because upper shore species respond more to upward extension of the damp zone than lower shore species, intertidal zones or belts are often differentially broadened (Lewis 1968). This has been extensively documented by Lewis (1964, 1968) for European shores and more recently by Tsuchiya (1979) in Mutsu Bay, Japan. The latter investigator found that the upper limits of the three major zones at a protected site were depressed below those at a nearby exposed site.

Topography and substratum can also modify patterns of vertical zonation. Topography can reduce the impact of breaking waves, resulting in the same effects mentioned above. Gently sloping benches may drain more slowly, resulting in extension of the upper boundaries of lower intertidal forms. Low-intertidal/shallow subtidal forms can inhabit higher level tidepools formed by depressions in the substratum. For example, Menge (1976) found that crevices extended the upper limit of mussels to higher than usual levels. Seapy and Littler (1978) compared patterns of vertical zonation at two adjacent intertidal sites in central California differing in the degree of exposure, slope of the shoreline, and type of substrate. The sea stack site was directly exposed to the prevailing seas and had a slope of 22.4 degrees. Zonation patterns of plants and animals were vertically distinct with little or no horizontal variation. From high- to low-tide levels, the zones were: *Balanus/Chthamalus, Mytilus/Pollicipes, Endocladia,* and various algae (Table 1). The adjacent boulder field was protected from the sea by offshore rocks and had a slope of less than 4.4 degrees. At this site, the zones were vertically indistinct and were the product of tidal height and horizontal beach slope and breadth. Going horizontally from the shore to sea, the "zones" were: *Hesperophycus/Endocladia* and *Chthamalus*; *Pelvetia/Endocladia* and *Chthamalus*; and *Endocladia/Mastocarpus papillatus.*

The presence of sand in rocky intertidal areas can modify vertical zonation. Frank (1965) found that the lower limit of limpets was determined by sand movement at a site in Oregon. The lower boundary of mussels and barnacles in New Hampshire was associated with the highest summer level of sand burial (Daly and Mathieson 1977). Cimberg (1975) found that sand burial set the lower limit of distribution of mussels at a site in northern California, and Littler et al. (1983) found that on Santa Cruz Island in southern California, the lower limits of mussels, black abalones, and owl limpets (*Lottia gigantea*) were determined by the physical smothering action of sand, rather than by the kinds of biological factors documented for other rocky intertidal habitats. Finally, aspect, or the degree of insolation, can influence patterns of vertical zonation. The barnacle *Tesseropora purpurascens* on the rocky shores of New South Wales, Australia, is restricted to shaded areas because of the inability of newly settled larvae to survive the high temperatures and desiccation of sunny habitats (Denley and Underwood 1979). Lower shore species may also be uplifted on shaded surfaces (Lewis 1964).

3. Horizontal Zonation

In sharp contrast to the voluminous literature on vertical zonation of rocky shores, there is very little published information on horizontal zonation patterns except for descriptions of exposed versus sheltered areas (e.g., Ricketts et al. 1985). This is unfortunate because shores that have horizontal gradients are common and because understanding mechanisms leading to horizontal zonation may yield new insights into mechanisms that regulate species distributions in marine systems in general.

Distinct zonation patterns have been found on flat shores, with boundaries between assemblages correlated with distance from the sea. Factors associated with distance included wave exposure (Marsh and Hodgkin 1962) and bench topography (Lebednick et al. 1971; O'Clair and Chew 1971).

4. Variation within Zones

We have organized this section by mechanisms responsible for observed patterns of within-zone spatial variation, but recognize that such organization is arbitrary and artificial because patterns in nature are rarely attributable to a single factor. Indeed, in almost every study of within-zone variation that we reviewed, patterns were due to several factors interacting with one another in often complex ways. Nevertheless, to simplify the presentation of such a diverse topic we divide this section into four types of factors that can result in within-zone spatial variation: (1) biological interactions, (2) wave exposure, (3) disturbance, and (4) microhabitat variation. For the remainder of this section the phrase "spatial variation" refers to spatial variation within intertidal zones.

a. Biological Interactions

Menge (1983) made a case for the overriding importance of predation in structuring rocky intertidal communities in New England, and argued that different levels of diversity observed within and among communities structured by predation and biotic disturbances represent equilibria determined by factors that enhance predation intensity versus those that inhibit it. In southeastern Australia, predation is responsible for local reduction in densities of the limpet *Patelloida latistrigata* in areas of otherwise high densities (Creese 1982). Frank (1982) found that five species of limpets at Cape Arago, Oregon, were commonly seen on vertical surfaces, though usually not near where vertical and horizontal surfaces meet. He suggested that this was due to predation on these limpets by the Black Oystercatcher, *Haematopus bachmani*, that can feed effectively only on horizontal surfaces and low ledges. Mercurio et al. (1985) found that selection by visual predators (fish and birds) can maintain the spatial separation of two limpet species, with one found on mussels and the other on barnacles.

Both intra- and interspecific competition have been shown to cause variation in spatial distribution of intertidal animals. Barnes and Powell (1950) reported that intense crowding of barnacles (*Balanus crenatus* and *Semibalanus balanoides* [=*Balanus balanoides*]) on rocky shores of the Firth of Clyde, Scotland, lead to the formation of hummocks in the barnacle cover. These hummocks were torn loose by wave action within the first year of settlement. Menge (1976) and Grant (1977) found that bare patches in the *Semibalanus balanoides*-dominated high intertidal zone at a site in New England were usually due to similar intraspecific competition for space among barnacles. Fucoids were generally absent from exposed sites, possibly due to competitive exclusion by mussels (Menge 1976). The mosaic of patches of *S. balanoides*, *M. edulis*, and *Fucus vesiculosis*, which characterize the transitional region between mid- and high-intertidal zones on rocky headlands in Maine, are partially due to the patchy distribution of overgrowth leading to density-dependent mortality (Grant 1977). Haven (1971) found that on exposed granite shores of Pacific Grove, California, the limpet *C. scabra* occurs on horizontal surfaces and vertical surfaces, while *C. digitalis* is largely restricted to vertical surfaces and overhangs. Where both species co-occur on vertical surfaces, *C. digitalis* is higher than *C. scabra*, and individuals of *C. scabra* are smaller than their conspecifics on horizontal surfaces. He suggested that interspecific competition may partly explain these differences in microhabitat distribution.

Species that provide shelter for other species create small-scale patchiness within intertidal zones. Glynn (1965) found that 93 different species were associated with clumps of the red alga *Endocladia muricata*, and Hill (1980) and Gunnill (1983) found a diverse and abundant fauna associated with the brown alga *Pelvetia fastigiata* in southern California. Mussel beds provide environments that trap sediment and detritus. These microhabitats provide food and shelter for a wide variety of species that form the "mussel community" (Reish 1964; Suchanek 1979; Kanter 1980).

Spatial variation can also be due to the effect of biological characteristics of the substratum on patterns of larval recruitment. On rocky shores of southeastern Australia, areas exposed to intermediate wave exposure consist of a mixture of two patch types, one dominated by barnacles and the other grazed bare by limpets. The configuration of the patchwork at any particular place or time depends upon the last period of intense recruitment and on the interactions between the adults and recruits (Underwood et al. 1983). Suchanek (1978) found that *Mytilus edulis* larvae could invade and dominate patches of bare space in beds of *M. californianus* on the exposed coast of Washington. Due to selective predation by gastropods, however, *M. edulis* is eventually replaced by *M. californianus*.

b. Wave Exposure

The extent to which rocky shores are exposed to the forces of breaking waves has an overriding influence on the spatial variation of intertidal animals. On Carnac Island in western Australia, Marsh and Hodgkin (1962) found the most diverse fauna in wave-exposed areas. Lewis (1968) reviewed European work related to patterns of spatial variation created by variations in wave exposure, and found that four types of mechanisms were important: (1) the morphology of species characteristic of protected areas cannot withstand the mechanical stress of strong wave exposure; (2) species characteristic of protected areas outcompete species typically found in exposed habitats; (3) sheltered sites are subject to levels of siltation that are not tolerable by species in exposed habitats; (4) species characteristic of exposed sites are excluded from protected sites because their propagules do not reach protected areas in sufficient numbers. Denny et al. (1985) discussed the mechanical limits to the size of organisms on exposed shores.

Recent work has shown that one of the more profound ways that wave exposure exerts its influence on community structure is by modifying the degree to which predation versus competition exert their effects. In other words, variation in wave exposure can lead to variation in the relative importance of competition versus predation (Connell 1975; Peterson 1979; Menge 1983), which in turn can produce spatial variation. In areas of high exposure to wave shock, the predatory activity of *Thais lapillus* in the mid-intertidal is restricted to crevices. Consequently its prey (mussels and barnacles) are widely distributed in these habitats but are absent from crevices (Menge 1978). In protected areas, predation intensity is greater and prey abundance is kept below levels where competition can occur. These areas may have significant amounts of bare space (Menge 1976), or they may be dominated by predation-resistant species such as algae that are unpalatable to herbivores (Lubchenco and Menge 1978). At intermediate sites, spatial variation is much greater because competition and predation interact to form a patchwork of species assemblages (Menge 1976; Lubchenco and Menge 1978). Peterson (1979) also found that competition was the most important factor structuring intertidal animal communities at an exposed site in New Jersey, while predation (especially by crabs) was most important in a nearby, protected site. Rocky shores of southeastern Australia exposed to wave shock are dominated by barnacles, apparently because wave-induced water motion inhibits barnacle predation by the whelk *Morula marginalba*. At protected sites, adult barnacles are rare due to high predation pressure by whelks, but grazing molluscs are abundant. Recruitment into populations of these grazers is apparently high enough to balance mortality from predation (Underwood et al. 1983).

Wave exposure can influence spatial variation in other ways as well. The species composition of mussel communities in southern California depends upon the degree of exposure to wave shock (Harger 1972). In protected areas the bay mussel, *Mytilus edulis,* dominates mussel clumps because silt accumulates inside the clumps and smothers *M. californianus. Mytilus edulis* avoids this stress by active movement toward the outside of the clumps. In exposed areas, *M. californianus* dominates because its growth rate is higher than that of *M. edulis.* The latter are incorporated into the matrix of the clump and suffocate (Harger 1970*a*). In areas of intermediate exposure the two species co-occur in varying relative abundances (Harger 1972). In this case, spatial variation in the species composition of mussel communities is primarily a function of wave shock through its influence on siltation and the competitive abilities of the two species involved.

c. Disturbance

Natural disturbance, or any natural event that creates space for colonization, is reviewed in detail in Section IV. Here we restrict our discussion to a few examples of localized mass mortality that are particularly important to variation within zones. Many of the factors that we have just discussed can be considered disturbances since they cause local removal of organisms. For example, predation can cause local extinction in populations of *Patelloida latistrigata* in southeastern Australia (Creese 1982), and competition for space in the barnacle zone produces hummocks that are then torn loose by wave action (Menge 1976).

According to Dayton (1971), the high degree of spatial variation in the barnacle/mussel assemblage on the coast of Washington state is due to continuous physical and biological disturbance preventing complete monopolization of space by any one species. The disturbances he identified were grazing by limpets, predation by carnivorous gastropods and sea stars, and battering by wave-propelled logs. Paine and Levin (1981) proposed a model describing the composition of mussel communities of the outer coast of Washington as a mosaic of patches of various ages and sizes in various stages of recovery. These patches are created by disturbances, including battering by logs, mortality due to freezing, and shearing stress of waves. The timing and magnitude of disturbances contribute further to spatial variation within the mussel community. The structure of the mid-intertidal zone of Mehuin, Chile, has also been explained in terms of disturbance regimes (Jara and Moreno 1984). Disturbance from wave action may also have varying effects on mortality of sessile organisms depending on the friability or hardness of the substratum (Page 1986).

Disturbances—in the form of limpet grazing, waves, waveborne rocks, and heat stress—resulted in highly variable species composition among tidepools at a given tidal height on the outer coast of Washington (Dethier 1984). In protected areas of the Santa Barbara coast, *Mytilus edulis* could potentially dominate all mussel communities, but it does not because of high mortality from storm-generated waves. Its congener *M. californianus* is more resistant to wave disturbance and enjoys a temporary dominance after storms. During subsequent periods of calm weather, cleared areas are recolonized by barnacles and ultimately *M. edulis* (Harger 1970*a, b,* 1972). Spatial variation in the species composition of the mussel community in this region is thus the result of storm-mediated mortality of *M. edulis* and subsequent recovery. Other disturbance agents that result in spatial variation in animal distribution include sand scour (Marsh and Hodgkin 1962), grazing and territorial behavior of limpets (Stimpson 1970), grazing by littorines (Petraitis 1983), and mechanical stress by harbor seals (Boal 1980).

d. Microhabitat Variation

Substratum heterogeneity (Grant 1977; Petraitis 1983), degree of insolation (Denley and Underwood 1979), water flow (Lewis 1968), and desiccation (Kensler 1967; Haven 1971) have all been shown to contribute to microhabitat variation. Tidepools contribute to small-scale spatial variation by providing discrete patches in which environmental factors differ from surrounding areas. Dethier (1984) found that tidepools at a given vertical height on the exposed coast of Washington could be dominated by any one of six species, and at no time were more than 20–50% of the pools dominated by the same species. Animals themselves can modify microenvironmental conditions and thus contribute to small-scale spatial variation. By creating a moist microenvironment in the desiccated and thermally stressed upper intertidal levels, the anemone *Anthopleura elegantissima* allows the development of coralline algae and populations of small sand tube worms (*Phragmatopoma californica*) at higher levels than they would normally occur (Taylor and Littler 1982). The positive correlation between densities of the limpet *Patelloida latistrigata* and the barnacle *Tesseropora rosea* is at least partially due to protection from desiccation afforded by the barnacles (Creese 1982).

Spatial variation within zones on rocky intertidal shores is clearly an integral part of these communities. The underlying mechanisms leading to spatial variation are related to a myriad of both physical and biological factors and their interrelationships, with patchiness created by disturbance, and subsequent succession of particular importance. Because a variety of phenomena will directly influence succession, we should recognize that succession will indeed be complex, and that generalizations about it should be made with caution.

B. Temporal Variation

1. Within Years

Daily, tidal, and seasonal changes in climate influence intertidal animals in a variety of ways. Winter storms normally remove old or unstable sessile animals (e.g., mussels, barnacles, and honeycomb tubeworms; Harger and Landenberger 1971; Grant 1977; Mayer et al. 1981) and many plants used as habitat by animals (e.g., blades of algae and surfgrass with limpets and snails; Black 1976; Gunnill 1983). Such seasonal removal of intertidal organisms provides cleared areas for new recruits and is important in maintaining mosaics of different species in the rocky intertidal (Paine and Levin 1981). However, as pointed out by earlier workers (e.g., Hewatt 1937; MacGinitie 1938; Gislen 1943, 1944; Glynn 1965), seasonal fluctuations are moderate along the west coast of the U.S., and overall winter–summer differences in rocky intertidal communities are not marked. There was little seasonal change in abundances of animals, for example, in a 2-year quantitative study along the coast of Santa Cruz and San Mateo counties (Doyle and Pearse 1972; Pearse

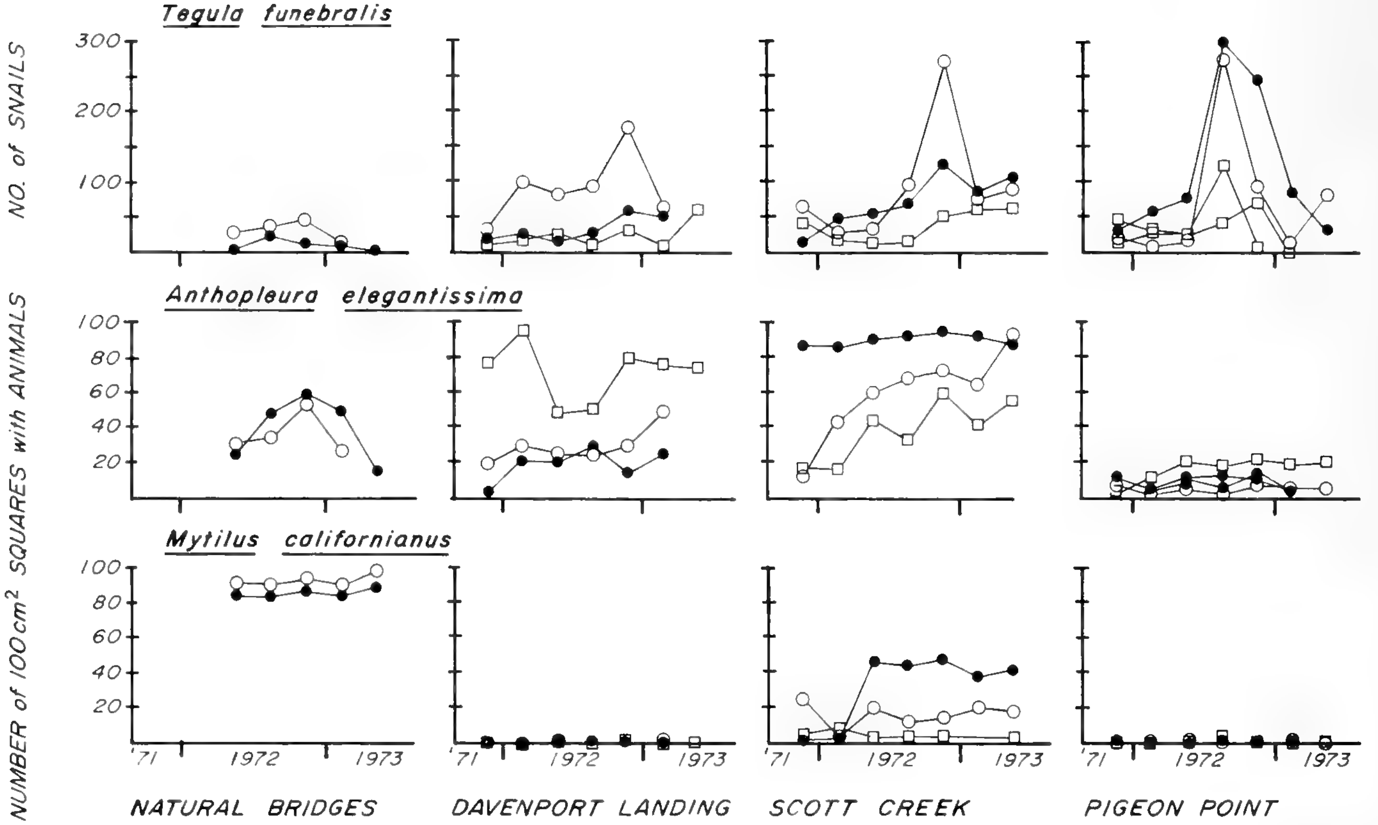


FIGURE 4. Changes over a 20-month period in abundance of turban snails (*Tegula funebralis*), cloning sea anemones (*Anthopleura elegantissima*), and mussels (*Mytilus californianus*) found in 1-m² quadrats placed in permanently marked positions in the mid zone of rocky intertidal benches at four sites on the Santa Cruz and San Mateo County coast. Abundance of snails estimated by counting total number of individuals in each quadrat; abundance of anemones and mussels estimated by scoring number of 100-cm² squares containing one or more animals (total number of squares = 100); each line (defined by symbols) represents changes in one quadrat. (Previously unpublished data of J. S. Pearse; collected with the assistance of students at the University of California, Santa Cruz, and with financial support from California Sea Grant.)

1980; Fig. 4). In a more detailed quantitative study of a mussel bed community at Santa Cruz, Beauchamp and Gowing (1982) found virtually no difference in animal species diversity or abundance in summer and winter.

Nevertheless, there are marked temporal changes or rhythms in the activities of many or most intertidal animals of central and northern California, as elsewhere (see general reviews in DeCoursey 1976; Naylor and Hartnoll 1979). In particular, feeding, growth, and reproductive activities of intertidal animals often display marked temporal patterns that are driven by daily, tidal, and/or seasonal rhythms. These activity patterns can have major impacts on patterns of distribution and abundance.

a. Feeding and Growth

Intertidal animals may be divided into two general categories with respect to their mode of feeding: (1) sessile and sedentary forms that capture or filter food particles from the water (suspension feeders) and (2) motile forms that move about in search of plant or animal prey. Suspension feeders feed only when they are covered with water so their feeding activity is largely regulated by tidal patterns. Most suspension feeders are stationary as adults, and their feeding activities might seem to have little or no impact on patterns of their distribution. However, because of the tidal rhythm, suspension-feeding animals living low in the intertidal can spend more time feeding than those living higher in the intertidal, and differences in feeding duration can cause differences in animal sizes. For example, Kopp (1979) found that differences in duration of feeding had a substantial effect on the growth and shape of mussels—those in lower areas had thinner and flatter shells because they were open and feeding for longer periods and grew outward more than those that were higher in the intertidal and closed most of the time. Similarly, feeding activity and growth form of some species of sea anemones are determined by the tidal rhythm—those living lower in the intertidal feed more and grow to larger individual sizes before dividing than those living higher in the intertidal (Bucklin 1981; Sebens 1983). Differences in food availability between sites at the same tidal height can also affect growth rates as suggested by Page (1986) for *Pollicipes polymerus*. Even feeding activity and growth of motile forms such as limpets are influenced by tidal rhythms, resulting in distinct distributional patterns of animal sizes (e.g., Sutherland 1970; Phillips 1981).

The activities of most animals that graze microalgae from rocks display a mixed daily/tidal rhythm, and actively graze mainly at night during low tides (e.g., crabs: Hiatt 1948; gastropods: Abbott et al. 1964, 1968; Stimpson 1970; Breen 1971, 1972; chitons: Burnett et al. 1975). Presumably this behavior is a response to insolation and desiccation, as well as bird predation (Frank 1982) during diurnal low tides, and perhaps to

fish predation or the threat of being swept away during high tides (night or day). Such behavior results in a short-term rhythm in the distribution of these animals, as they often rest in cryptic sites some distance from their feeding areas. Similarly, sea stars (*Pisaster ochraceus*) on the Washington coast have been noted by Mauzey (1966) and Dayton (1971) to forage upward during high tide and then return to lower levels to digest the captured prey, presumably avoiding desiccation during low tide.

The semimonthly, monthly, to semiannual tidal rhythms also modify the foraging areas of motile animals, particularly those that occur in the lower zones. During periods of neap tides, the lower tidal levels are exposed for only short periods, or not at all. This is particularly true in the northeastern Pacific in early fall (September) and early spring (March) when few tides extend below mean low water. Grazing snails (especially *Tegula brunnea*), predaceous snails (especially *Nucella emarginata*), and sea stars (*Pisaster ochraceus*) all tend to move higher into the intertidal during neap tide periods (P. K. Dayton, pers. comm.; J. S. Pearse, pers. obs.). As low spring tides become more extreme in the late fall (December) and late spring (June), these animals are exposed for progressively longer periods of time, and they move down. This sort of movement occurs even during a single spring tide series, so more individuals of motile animals are seen on the first days of a spring tide series than on later days (J. S. Pearse, pers. obs.).

Along the coast of Greenland (Petersen 1962), New England (Menge 1976; Grant 1977), Britain (Lewis 1964), the Antarctic Peninsula (Stockton 1973) and other places where there are freezing water temperatures, activities of many or most animals are severely curtailed in the winter. Such severe winters do not occur along most of the coast of western North America, but major storms, often with heavy rains, usually occur in the winter months and influence animal activities. For example, Frank (1965) found that the limpet *Collisella digitalis* tended to ascend in the intertidal of Oregon during fall and winter and descend in the spring. Similarly, Phillips (1981) found that the limpet *Notoacmea scutum* moved much more in central California during the summer and fall than in the winter and spring, and the mean vertical position of the animals was 33 cm higher in January, as the winter storms began, than in May. At least part of this activity was related to feeding and algal abundance; growth rate was highest in spring–summer when algal abundance was highest, and movement peaked in late summer as algal abundance decreased. Also on the coast of central California, turban snails (*Tegula funebralis*) were much more abundant on flat rock surfaces during the summer and fall than winter and spring (Fig. 4); presumably the snails, known to be long-lived (Frank 1975), nestled among cracks and boulders during the winter and then emerged to graze rocks after the winter storms subsided. Changes in turban snail densities in the open, however, were the only marked seasonal pattern of animal distribution and abundance noted during the 2-year study. This and other studies (e.g., Nybakken 1978; North et al. 1983) suggest that there is little seasonal change in the distributional patterns of most intertidal animals of central California. Even species that do undergo seasonal changes in activity farther north show little or no seasonal change in activity in central California. For example, while Mauzey (1966) found that individuals of the sea star *Pisaster ochraceus* stop feeding, clump together, and virtually hibernate in midwinter in Puget Sound, Feder (1970) could find no evidence of seasonal differences in feeding or distributional patterns by individuals of this species near Monterey.

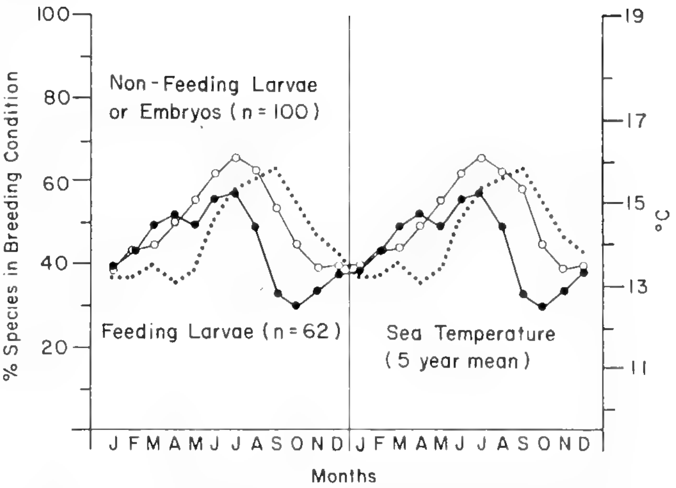


FIGURE 5. Changes in monthly mean sea water temperature (dotted line) and percentage of species of intertidal animals on the coast of central California in breeding condition (solid lines), divided between species with and without feeding (planktotrophic) larvae. Sea temperature records are 5-year means (1979–82, 1984) taken at the Joseph M. Long Marine Laboratory of the University of California, Santa Cruz. Reproductive data compiled by J. S. Pearse and S. Finch from accumulated information in Morris et al. (1980); *n*, number of species. The reproductive information is based both on literature reports and Professor Donald P. Abbott's 30 years' experience of teaching and research at Hopkins Marine Station; although the data on many of the individual species may be inconclusive, as an aggregate the body of information is probably an accurate reflection of the general pattern of breeding by intertidal animals in central California. Plotted over a 2-year period for clarity.

b. Reproduction

As is typical of shallow-water marine communities at temperate latitudes (Giese and Pearse 1974), most species in the rocky intertidal of the west coast of the U.S. have distinct reproductive periods (Hewatt 1938; Houk 1973). In central California, over 50% of the species are full of gametes and in breeding condition in the spring and summer (Fig. 5). A group of species with feeding (planktotrophic) larvae are in breeding condition slightly earlier than most of those without feeding larvae (lecithotropic); one possibility is that feeding larvae of these species need to spend a month or so in the plankton before settling, and the time most suitable for settling and recruitment is about the same for most species, regardless of their mode of development.

The period when the lowest proportion of intertidal animals in central California are in breeding condition is in the fall (October–November; Fig. 5); in contrast to intertidal algae that are commonly reproductive in the fall (Section II). This is the time of lowest primary productivity and highest sea temperatures (Bolin and Abbott 1963), immediately preceding winter storms. Presumably all these factors select against many kinds of animal recruits, and for algal recruits. Nevertheless, even at this time of year between 30 and 40% of the animal species are in breeding condition, emphasizing the lack of overall seasonality along the coast of central California (Fig. 5).

Most species of intertidal invertebrates in central and northern California have pelagic larvae that drift and feed in the

plankton for days to months before settling. Because most spawn in the spring and summer (April–August; Fig. 5), their larvae would be expected to be present at about the same time. Few studies are available, however, to document the presence of larvae of intertidal species in the plankton. One such study is that of Grosberg (1982) who found larvae of acorn barnacles in the plankton in May. Moreover, these were stratified in the water; those of *Chthamalus* spp. were very near the surface while those of *B. glandula* were slightly deeper, corresponding to the adults' stratification on the shore. A more recent study in southern Monterey Bay has shown further that promontories, offshore rocks, and even offshore kelp forests can inhibit the onshore movement of larvae and cast "settlement shadows" where fewer barnacles settle and grow than on more exposed shores (Gaines and Roughgarden 1985). A demographic model by Roughgarden et al. (1985) further suggests that settlement rates can have profound effects on population structure. Such work, as well as Connell's (1985) recent review, indicates that larval recruitment patterns both in time and in space have an important, but still generally undefined, impact on adult distribution and abundance patterns (Lewin 1986).

Although a considerable body of descriptive information has accumulated over the past 25 years on gonadal growth and spawning cycles of intertidal invertebrates of central California, beginning in particular with the work of Giese and his students (Giese 1959), experimental work on factors regulating these cycles remains sparse. Most such work has been done on species of the north Atlantic and has indicated that changes in sea temperature are of prime importance for timing reproductive cycles (Giese and Pearse 1974). However, seasonal temperature changes are not marked on the west coast of the U.S., and there is little evidence that such changes directly influence seasonal reproductive activities of west coast intertidal species. There is evidence that seasonal changes in food supply influence temporal patterns of reproduction. For example, Sutherland (1970) found that individuals of the limpet *Collisella scabra* produce gametes throughout the year when they occur in the low zone at Bodega Bay, but other individuals living only a few meters higher, where algal production is restricted mainly to the spring, produce gametes only in the spring. In addition, recent work has shown that the reproductive cycles of common west coast intertidal sea stars and sea urchins are under photoperiodic control (Pearse and Eernisse 1982; Pearse et al. 1986*a, b*).

Environmental factors selecting for discrete reproductive periods, as opposed to environmental cues such as photoperiod that synchronize reproduction, remain particularly elusive, and because they act over long periods of evolutionary time, they cannot be investigated directly or experimentally. The predominance of reproductive activity among north Atlantic species in the summer is assumed to be a response to favorable summer temperature and food conditions for the developing larvae. The predominance of spring and summer reproduction by central California species, however, corresponds to the time of low to rising temperatures rather than the time of supposedly more favorable (higher) temperatures in the fall (Fig. 5). Moreover, although the spring upwelling provides a nutrient pulse that initiates the main seasonal phytoplankton bloom, animals that produce nonfeeding larvae tend to spawn at the same time as those with planktotrophic larvae. Himmelman (1975) found that substances associated with the spring phytoplankton bloom stimulated several species of chitons to spawn, even though chiton larvae do not feed on phytoplankton. Levels of dissolved organic material in the water may be higher during the plankton bloom than at other times, and nonfeeding larvae may use such dissolved organic material, as has been shown for some feeding larvae (e.g., Manahan et al. 1983). However, there have been no studies on the nutrition of nonfeeding larvae (but see Fenaux 1982), and the importance of such sources of nutrition is unknown.

Perhaps the most plausible evolutionary/ecological explanation for the predominance of spring–summer reproduction among intertidal animals of central California is that more space is open and available for settlement after the winter storms, especially if there is damage by logs and other floating debris to established communities, as found by Dayton (1971) for the outer coast of Washington state. The establishment and growth of juveniles in the resulting cleared areas would then be favored during the generally benign summer conditions that follow. Paine and Levin (1981) similarly suggest that many common species spawn in the winter because more space is available then for recruitment. In addition, the variable and generally weak current patterns in the summer (Griggs 1974) may tend to maintain larvae near the region of the adult populations that spawned them.

Because there is such variability among the spawning times of different species, the natural history of species must be well understood before much can be said about their particular temporal pattern of reproduction. For example, Hines (1978, 1979) found very different spawning times for the three common acorn barnacles of central California, and these corresponded to very different life history patterns that appeared well suited for different portions of the intertidal. Small gregarious individuals of *Chthamalus fissus* occur in the highest regions of the intertidal where they grow rapidly, reach sexual maturity within 3 months, and produce a brood of eggs approximately monthly until they are killed by adverse climatic conditions—usually within a few months. In contrast, large, mainly solitary individuals of *Tetraclita squamosa* occur in the lowest regions of the intertidal zone where they grow slowly, reach sexual maturity in about 3 years, and then produce a few broods of eggs each summer for many years, perhaps decades. Intermediate between these two species is *Balanus glandula* that is physiologically unable to survive in the higher portions of the intertidal where *C. fissus* predominates. However, *B. glandula* is quickly discovered and eaten by predators in the lower intertidal where the thick-shelled individuals of *T. squamosa* survive for so long. Juveniles of *B. glandula* recruit mainly in the spring, grow over the following year, and then produce several broods. Few survive for more than a year.

Even species that seasonally produce large numbers of gametes each year may not show any sort of predictable pattern of recruitment and population turnover. For example, although the purple sea urchin *Strongylocentrotus purpuratus* produces enormous numbers of gametes each winter and early spring (Pearse 1981), the appearance of juveniles north of Point Conception is an unusual event. Ebert (1982*a*) found only one episode of recruitment of *S. purpuratus* in an intertidal area in southern Oregon over nearly 20 years. We also have noted only occasional recruitment of this species in central California. Recruitment in southern and Baja California is a much more pre-

dictable event, with numerous recruits being noted nearly every year (Pearse et al. 1970; Ebert 1982*b*). The reason for this difference in recruitment between the northern and southern portions of the range of *S. purpuratus* is unknown, as is the reason why some years are "good" and others "bad" for recruitment; the differences are perhaps due to regional and year-to-year differences in current patterns related to year-to-year variations in the California Current (Chelton et al. 1982). Other intertidal species also have been noted to recruit more regularly in the southern part of their range (southern and central California) than in more northerly regions (Oregon, Washington)—for example, the turban snail *Tegula funebralis* (see Frank 1975), and the file limpet *Notoacmea scutum* (see Phillips 1981). However, some of these trends may be an artifact of looking at only a few sites. T. A. Ebert (pers. comm.), who recently examined 25 sites between Baja California and Oregon, suggests that differences in *S. purpuratus* recruitment between nearby sites may be greater than between latitudes.

2. Between Years

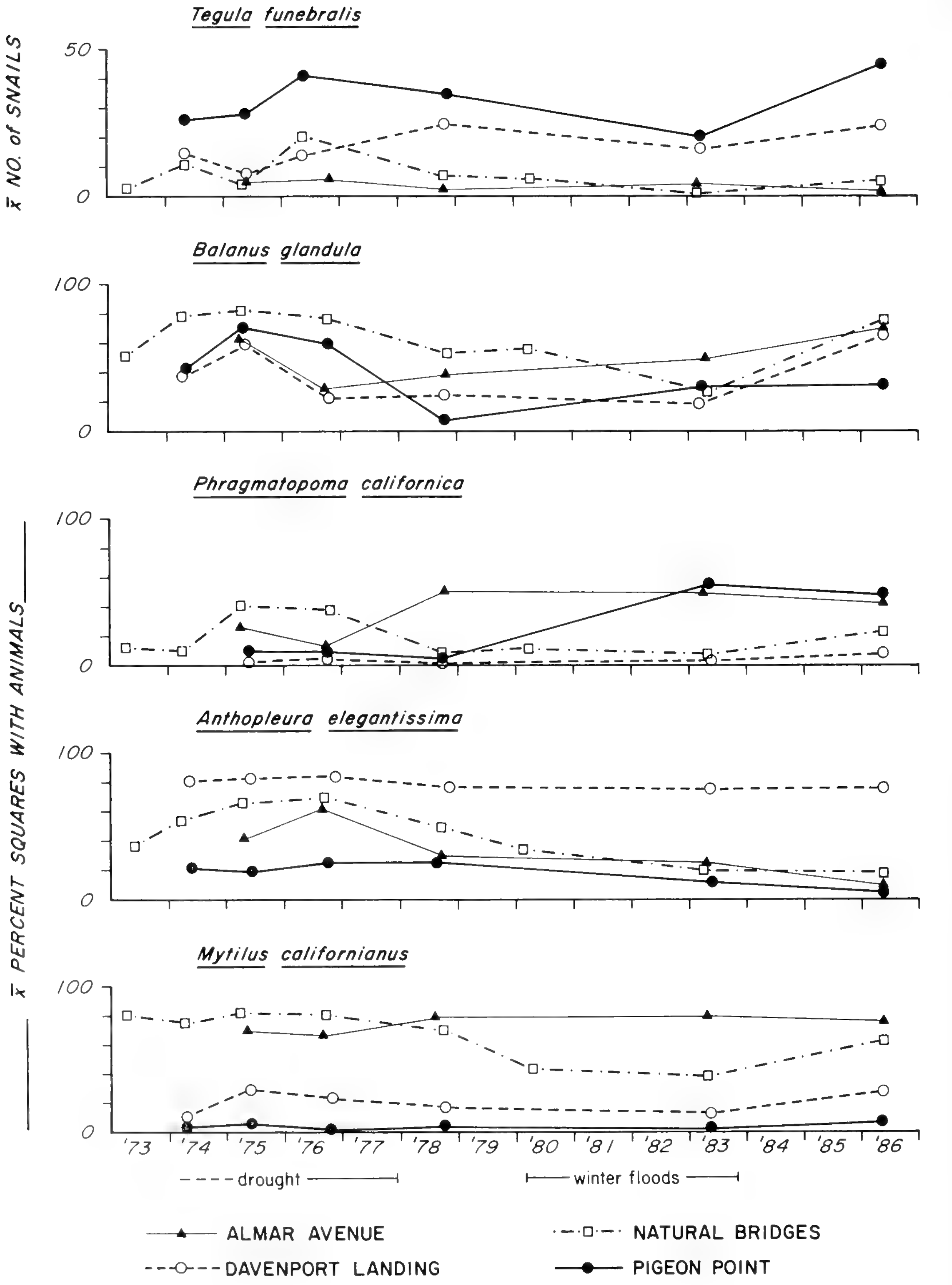
Although tidal and seasonal patterns of change have been detected and studied in a variety of species and processes, as noted above, much less information is available about long-term patterns of change in animal populations. The reason for this lack of information is clear: detection and documentation of long-term change usually demand the maintenance of well-designed, long-term monitoring programs. Such programs are rare (e.g., Coe 1956; Jones et al. 1979; North et al. 1983; PGE 1984; Hartnoll and Hawkins 1985; Paine et al. 1985). Like those collecting weather data, monitoring programs can continue for years without showing dramatic or clearly delineated patterns of change. Thus, they instill little enthusiasm either from granting agencies or ambitious and creative investigators. Consequently, the literature contains reports of dramatic events, but little on background patterns that continue over most "normal" years (see discussion in Paine 1986). Reports of the impact of "El Niño" provide an example of this nonplanned type of investigation. Mass strandings of pelagic crabs on the beaches of central California were reported for the first time in a century after the 1958–59 El Niño (Glynn 1961), but it is not clear whether this was really an unusual event or simply the result of a conscientious observer reporting it. Mass strandings of these crabs were noted, for example, after the El Niño events of 1973 and 1983 (A. Baldridge, pers. comm.), but no reports of them were published. Moreover, few changes have been reported in the animal communities of the rocky intertidal during or following El Niño events, perhaps because careful monitoring programs were not in place to detect such change (it is also possible that intertidal plants and animals are insensitive to changes resulting from most El Niño conditions).

It is well recognized that winter storms vary in intensity, duration, and impact among different years, and such variation would be expected to cause considerable variation from year to year in the abundance and richness of intertidal life. When severe winter storms are in phase with periods of extreme spring tides in December and January, the impact can be particularly dramatic. For example, the severe winter storms of January 1982 led to major rock slides and shore erosion along the Big Sur coast, decimating at least one intertidal community that had been visited repeatedly the previous 4 years (Pearse 1984). The same storms, however, had little noticeable impact on rocky intertidal communities on the Monterey Peninsula or along the coast of Santa Cruz and southern San Mateo counties (J. S. Pearse, pers. obs.). Indeed, ongoing studies by students of the University of California, Santa Cruz, indicate that the abundance of major species of animals in these communities remained remarkably constant for over a decade, although their abundance varied from area to area (Fig. 6).

Long-term studies at Diablo Canyon have shown that sand scouring and boulder movement during winter storms produce barren patches of substratum that are subsequently recolonized by invertebrates and algae, and the extent of change is related to storm intensity (Mayer et al. 1981). Similar effects by irregular seasonal sand movement have been noted at San Nicholas Island (Littler et al. 1983), as well as in New England (Daly and Mathieson 1977). Conversely, North et al. (1983) qualitatively monitored the same area at Diablo Canyon between 1969 and 1982, and did not detect any obvious difference in distributional patterns of the major species present.

The above studies indicate that rocky intertidal communities can remain relatively unchanged for periods of over a decade, even when substantial storms occur. Similarly, distributional patterns of animals in other rocky intertidal areas that have been studied for moderate lengths of time appear to remain relatively unchanged (e.g., Washington state: Connell 1970; Paine 1974, 1976, 1984; Paine and Levin 1981; Isle of Man: Hartnoll and Hawkins 1985). Moreover, activities such as annual rhythms of reproduction, although showing some variation among different years, maintain considerable stability as shown by decade-long records for the chiton *Katharina tunicata* (Giese 1969) and the sea star *Pisaster ochraceus* (Halberg et al. 1969). In contrast, Caffey (1985) found that recruitment and early mortality of the barnacle *Tesseropora rosea* varied significantly at all spatial and temporal scales examined on Australian shores. Connell (1985) found that there is great variability in larval recruitment from year to year of barnacles, limpets, clams, and sea stars, but particular sites maintain consistently higher recruitment levels than others. Thus, although still not unequivocally demonstrated, differences among sites may be related directly to differences in recruitment.

However, observations that span times greater than a decade or so indicate that abundances and distributional patterns of animals can change dramatically over time. J. H. Connell (pers. comm.), for example, has noted that intertidal boulder fields studied by his students near the campus of the University of California, Santa Barbara, have changed dramatically over the past dozen years due to invasion by sand-encrusted aggregations of *Phragmatopoma californica*. Similar changes have been noted near Santa Cruz as dense aggregations of these polychaetes alternatingly form and disappear over large areas of the rocky intertidal (J. S. Pearse, pers. obs.; see also Fig. 6). On a longer time scale, Hewatt (1935, 1937) and MacGinitie (1938) described extensive mussel beds at Hopkins Marine Station in southern Monterey Bay in the mid-1930s that had nearly disappeared by the late 1960s (D. P. Abbott, pers. comm.; M. S. Foster, C. Harrold, J. S. Pearse, pers. obs.). Although mussel beds are known to undergo small fluctuations in some other areas due to storms (Paine and Levin 1981) or perhaps in relation to changes in water temperature (Coe 1956), the dramatic



Tegula funebralis
x̄ NO. of SNAILS
50
0
Balanus glandula
100
0
Phragmatopoma californica
100
0
Anthopleura elegantissima
100
0
Mytilus californianus
100
0
x̄ PERCENT SQUARES WITH ANIMALS
'73 '74 '75 '76 '77 '78 '79 '80 '81 '82 '83 '84 '85 '86
drought
winter floods
ALMAR AVENUE
NATURAL BRIDGES
DAVENPORT LANDING
PIGEON POINT

reduction in the mussel bed cover at Hopkins Marine Station almost certainly was due to predation by sea otters. These animals returned to Monterey Bay in the 1960s after being nearly exterminated in the previous century. Changes in the abundance of mussels and other shellfish that are preyed upon by sea otters also have been noted elsewhere along the coast of western North America after the sea otters' return, as recently summarized by Estes and Van Blaricom (1985). Dramatic changes in community organization over periods of hundreds to thousands of years related to human activities and sea otters also have been documented at some sites in the Aleutian Islands (Simenstad et al. 1978).

Other causes of long-term changes in community organization also are undoubtedly important, although their identification has been difficult. Sergin (1980), for example, suggested that the precession of the earth's orbit causes long-term oscillations of climate and seasonal timing of the tides; these could lead to long-term, cyclic changes in intertidal communities. Moreover, Gray and Christie (1983) showed that cycles of 3–4, 6–7, 10–11, 18–20, and about 100 years can be detected in hydrographic data, and that many benthic species respond to the long-term cycles. Nevertheless, predicting long-term changes in communities by following these cycles may be an unattainable goal due to the long periods involved; Gray and Christie (1983) presented evidence for cycles with periods of over 4,000 years.

Noncyclic events, which by definition are unpredictable, also could lead to dramatic changes in community organization. Examples include: (1) catastrophic disease that removes important members of intertidal communities, as occurred in the Gulf of California (Dungan et al. 1982); (2) large-scale variations in the flow of the California Current that cause large-scale variations in the biomass of zooplankton along the coast of western North America (Chelton et al. 1982); (3) earthquakes and other geological disturbances that dramatically modify the underlying topography, as occurred in Alaska (Haven 1972; Johansen 1972; Lebednik 1973); (4) catastrophic oil spills that can alter intertidal areas for a decade, as occurred on the southwestern coast of Britain after the Torrey Canyon spill (Southward 1979; Section V).

Long-term changes in animal distribution and abundance in the rocky intertidal zone can thus be expected to result from predictable (cyclic) and unpredictable biotic and abiotic changes. The resulting altered communities may eventually revert to the earlier state of "dynamic equilibrium," as found by Southward (1979) after the Torrey Canyon spill. Hartnoll and Hawkins (1985) present evidence that such an equilibrium exists on the rocky shores of the Isle of Mann where the abundances and spatial patterns of the major species fluctuate with approximately a 7-year cycle. Simenstad et al. (1978) further proposed that there may be "several stable state communities," and disturbances can shift communities from one stable state to another. On the other hand, Connell and Sousa (1983) reviewed the evidence for community stability and persistence and found little support for the idea of natural point equilibriums, and no unequivocal examples of multiple steady states in unexploited natural populations or communities. Rather, they found that natural populations, including those of the rocky intertidal, show considerable temporal variability within stochastically defined bounds. Long-term monitoring studies, as established at Diablo Canyon in central California (Mayer et al. 1981; North et al. 1983; PGE 1984) and on the coast of Britain (Lewis 1977; Jones et al. 1979), appear to be crucial for resolving whether natural equilibriums actually occur or, if not, what the range is of temporal variation in intertidal communities.

IV. Effects of Natural Disturbance

In the previous sections we have reviewed patterns in rocky intertidal communities and the processes that cause these patterns at various spatial and temporal scales. In the few assemblages so far examined, and particularly at the scales of within assemblages and between years, much of the variation in patterns of distribution and abundance appears to result from disturbances that, by definition, remove parts of, or entire assemblages of sessile organisms. This produces space for potential colonists and thus initiates succession (Foster and Sousa 1985; Sousa 1985). Disturbances may account for much of the pattern in the rocky intertidal zone (Dayton 1971; Sousa 1979*a*, 1984, 1985; Paine and Levin 1981). They may also be in part responsible for local differences in diversity (Lubchenco 1978; Sousa 1979*b*; Section III) and for the presence of at least one annual (Paine 1979) and various ephemeral species that require newly cleared space for colonization (fugitive species: Sousa 1984, 1985). A greater appreciation of the real and potential effects of disturbance on community structure, combined with a more thorough understanding of the mechanisms that create variability during succession, has also made many of the traditional paradigms "explaining" community structure questionable (Connell 1972, 1980; Connell and Slatyer 1977; Connell and Sousa 1983).

The relationship between disturbance and patterns in rocky intertidal communities has recently been reviewed by Sousa (1985), and biological disturbance (e.g., removal of algae by grazers) has been discussed in previous sections. We will confine our discussion below to physical disturbance, and to succession after both biological and physical disturbance. Finally, a note of caution about the evidence for successional processes, particularly the relationship of recovery from experimental disturbances versus natural ones, is warranted. In the majority of successional studies on rocky intertidal shores, sessile organisms

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Figure 6. Changes in mean abundance of turban snails (*Tegula funebralis*), acorn barnacles (*Balanus glandula*), honeycomb tubeworms (*Phragmatopoma californica*), cloning sea anemones (*Anthopleura elegantissima*), and mussels (*Mytilus californianus*) over a 13-year period in the mid zone of four contrasting intertidal rocky benches on the coast of Santa Cruz and San Mateo counties. The Almar Avenue and Natural Bridges sites were visually dominated by mussels and, periodically, by honeycomb tubeworms, that at Davenport Landing by cloning sea anemones, and that at Pigeon Point by the alga *Mastocarpus papillatus*. At each site, permanently delineated areas about 2,500 or 5,000 m^2 were sampled with 12–30 randomly placed 0.25-m^2 quadrats. The quadrats were divided by monofilament thread into 25 100-cm^2 squares and the number of squares occupied by sessile plants and animals was scored; the total number of snails and other large motile animals was counted for each quadrat. (Previously unpublished data of J. S. Pearse; collected with the assistance of students at the University of California, Santa Cruz, and with financial support from California Sea Grant.)

TABLE 5. RESULTS OF SUCCESSIONAL STUDIES IN THE NORTHEASTERN PACIFIC THAT USED TOTAL CLEARING.

Location	—Assemblage cleared —Time of clearing —Number of clearings —Size of clearings —Time observed	Recovery time	Reference —Notes
La Jolla, California	—Not defined —January 1923 —3 —30 × 60 cm and 1 91-cm-diam. pool —4 mo	≫4 mo	Wilson (1925) —Most of the common algae did not reappear in clearings
Friday Harbor, Washington	—Barnacles/limpets —June 1925 —6 clean rocks placed along each of 2 transects —Rocks ~25 cm diam. —43 days	~1 mo	Pierron and Huang (1926) —Recovery based on rocky transect only —After 43 days, more barnacles and snails on clean rocks than undisturbed rocks
Monterey, California	—*Mytilus californianus* —November 1931 —1 —91 × 91 cm —2.5 yr	>2.5 yr	Hewatt (1935) —Mussels recruited after 5 mo but abundance still low at last observation; richness of associated species also still low
Monterey, California	—*Endocladia*/*Mastocarpus papillatus* (1), *Rhodoglossum* (2), *Iridaea flaccida* (3), *Rhodymenia pacifica* (4) —2 seasons, 1944 —3 transects in January, 1 each in April, July, and October —30-cm-wide strips —9–27 mo	(1) >27 mo/~18 mo (2) 6–9 mo (3) ~6 mo (4) 9–12 mo	Northcraft (1948) —Recovery estimated by similarity to preclearing abundance
Yoakam Point, Oregon	—*Mytilus californianus* (1), *Iridaea flaccida* (2), *Odonthlia* (3) —2 transects, 1 in 1958, 1 in 1960 —1-m-wide strips —6–8 yr	(1) >8 yr (2 and 3) 2 yr	Castenholz (1967)
Olympic Peninsula, Washington	—*Fucus distichus* —November–December 1966 —3 large rocks —Size not given —2.5 yr	>4 yr	Dayton (1971)
Eureka, California	—*Collisella*/*Balanus* (1), *Mytilus californianus* (2), *Chthamalus* (3) —October 1968 —2 transects through zones —10 cm wide —36 mo	(1) 2 mo/36 mo (2) >36 mo (3) 3 mo	Cimberg (1975) —Recovery based on index of redevelopment relative to controls; *M. californianus* settled 2 mo after clearing but eaten by *Pisaster*, 40% recovery of organisms in mussel zone in 36 mo; recovery inversely proportional to size of largest invertebrate in zone
San Diego, California	—*Lithothrix* —Seasonally, 1973–74 —3 quadrats/season —0.05-m² quadrats —1 yr for each set of seasonal clearings	*Lithothrix* cover > 1 yr Species richness 1–4 mo	Emerson and Zedler (1978) —Colonization of some species varied with season; *Lithothrix* recruited quickly but grew slowly
San Clemente Island, California	—*Gigartina canaliculata*/*Corallina officinalis* (1), blue-greens/*Ulva*, *Pseudolithoderma* (2) —December 1974 —3 in each assemblage —0.15-m² plots —30 mo	(1) >30 mo (2) 1 mo	Murray and Littler (1978) —Blue-green assemblage in area polluted by sewage; recovery based on similarity to controls, (1) almost recovered in 30 mo
Twelve sites in southern California	—Varied depending on site —1975–77, various seasons —1–40 tidal height —1-m² quadrats —12–24 mo	>24 mo	Murray and Littler (1979) —Scraping left some encrusting organisms; plants recover faster than animals; high intertidal perennial algae and large sessile animals slow to recover
Santa Barbara, California	—*Gigartina canaliculata* —February 1975 —12 blocks, "a number" of clearings —165-cm² blocks and 100-cm² clearings —30–36 mo	2–3 yr	Sousa (1979*a*) —Recovery faster in clearings due to vegetative growth from edges

TABLE 5. CONTINUED.

Location	—Assemblage cleared —Time of clearing —Number of clearings —Size of clearings —Time observed	Recovery time	Reference —Notes
Tatoosh Island, Washington	—*Mytilus californianus* —Various times —Various replications —Various sizes —5.5 yr	5–7 yr if recover via recruitment	Paine and Levin (1981) —Small (< 10 m^2) patches recover more quickly because of migration
Monterey, California	—*Endocladia/Pseudolithophyllum* (1), *Iridaea flaccida/Tetraclita* (2), *Prionitis* spp. (3) —(1 and 2) October 1973, (3) October 1973 and May 1974 —6/assemblage —20 × 20-cm quadrats —27 mo plus miscellaneous observations for 7 yr	(1) ~4 yr (2) ~24 mo (3) >7 yr	Foster (1982) and unpublished data —Recovery based on cover of dominant plants relative to controls
Bodega Head, California	—*Mytilus californianus* —July 1979 —16 of each —25 × 25- and 50 × 50-cm quadrats —36 mo	≫3 yr	Sousa (1984) —No *M. californianus* recruitment in 3 yr but some recovery by migration; some algal species on tops of mussels recruited into clearings within 12 mo (*Gigartina, Pelvetiopsis*); *Endocladia* recruited but not back to preclearing abundance after 36 mo

have been completely removed from experimental areas. However, as discussed by Foster and Sousa (1985), most natural disturbances result in less than complete removal, particularly of plants. Since what is left behind may regrow and/or affect colonization by other species, subsequent succession and recovery rates may be quite different from those found in total clearings. Moreover, the time of disturbance, its areal extent, position relative to sources of recruits, etc., all may affect succession (Foster and Sousa 1985). With the possible exception of mussel beds (Paine and Levin 1981; Sousa 1984), the importance of these parameters to intertidal succession remains unknown for most assemblages (Pickett and White [1985] reviewed the relationship between these parameters and succession in other habitats).

A. Experimental Disturbance

1. Complete Clearing

Complete removal of organisms from experimental plots has been done to describe succession in particular areas, to investigate factors that may affect succession, and to estimate recovery rates. Most intertidal studies (see references in Table 5) have found a successional sequence that begins with ephemeral diatoms, green, and/or blue-green algae. These organisms are commonly replaced by longer-lived, perennial species more characteristic of the assemblage in which the clearings were originally made. This process was traditionally thought to be facilitative; early colonists created microenvironments necessary for the establishment of later species (e.g., Northcraft 1948). However, evidence from both intertidal (Lee 1966; Sousa 1979*a*, 1980; Foster 1982) and subtidal (Foster 1975; Connell and Slatyer 1977) studies indicates that early colonists may inhibit or have little effect on later species. The low intertidal *Phyllospadix* spp. assemblage is one exception; the seeds of surf grass are adapted for recruiting to the branches of other plants (Dawson 1966) and Turner (1983*a*) has shown that plants such as articulated corallines do facilitate surf grass recruitment.

If cleared areas suffer no further physical disturbance, the factors that affect subsequent succession include recruitment, growth, and survival of colonizing species (Northcraft 1948; Emerson and Zedler 1978; Sections II and III), grazing (Sousa 1979*a*, 1984; Foster 1982; MacLulich 1986), predation (Cimberg 1975), and factors associated with clearing size (grazing, dispersal: Sousa 1984, 1985). These factors have all been shown to be important in one study or another, but there has not been enough replication of appropriate experiments in space and time to suggest some interactive model or even a ranking of factors important to rocky intertidal succession.

As might be expected given the diversity of organisms and processes that occur in the rocky intertidal zone, reported recovery rates, even within one assemblage, are highly variable. Table 5 summarizes recovery rates found or estimated in succession studies done between British Columbia and Baja California using complete clearings. Although the places, times, and sizes of clearing are often different, these studies support Murray and Littler's (1979) conclusion that assemblages dominated by plants generally recover faster than those dominated by animals. The exception appears to be high intertidal barnacle assemblages that may recover in less than 1 year. Among assemblages dominated by perennial plants, those in the high intertidal appear to recover more slowly than those lower on the shore. Again, *Phyllospadix* spp. may be an exception since recruitment is facilitated by the presence of perennial algae that must first become established after clearing (Turner 1983*b*), and most recovery occurs by the slow vegetative ingrowth of surrounding rhizomes (Turner 1985).

As found by Sousa (1980, 1984), the above generalizations are consistent with what is known about dispersal, recruitment, and growth of the organisms involved (Sections II and III). Perennial algae appear to recruit from fairly local parental stocks and the planktonic life of the propagules is probably short (Sousa 1984). Growth conditions for plants are generally less favorable higher on the shore (Underwood 1980; Underwood and Jernakoff 1981; Foster 1982; Cubit 1984). Long-lived sessile animals appear to have highly variable recruitment and grow relatively slowly (Section III). The recruitment of some animals, like *Mytilus* spp., may be enhanced by perennial algae such as *Endocladia muricata* that are slow to recover (Table 5).

2. Partial Clearing

Partial clearings have generally been done to determine the effects of a particular organism, usually the cover or numerical dominant in a given assemblage, on associated species. This type of clearing is quite different from complete removal because the remnants of organisms left behind may regrow, increasing the recovery rate. Organisms left in partial clearings may inhibit (Lubchenco 1980; Foster 1982) or enhance (Barnes and Gonor 1973) later recruitment into cleared areas. Removal of canopy species such as *Hedophyllum sessile* or *Pelvetia fastigiata* can alter microclimates or topography such that understory organisms die or migrate from the clearings (Dayton 1975; Hill 1980) or increase in abundance if growth is inhibited by the canopy (Dayton 1971).

Partial clearings are more similar to most natural disturbances in rocky intertidal communities than are complete clearings (Foster and Sousa 1985; Sousa 1985). Natural disturbances such as moderate waves, exceptionally hot or cold weather during low tides, freshwater runoff, etc., commonly remove only the upright parts of many seaweeds. When this is done experimentally, recovery to predisturbance cover is usually faster than after complete removal (*Fucus distichus*: Dayton 1971; articulated corallines: Murray and Littler 1979; *Phyllospadix scouleri*: Dethier 1984). This is not always the case as Hill (1980) found that *Pelvetia fastigiata* recovered at almost the same rate (completely in 38 months) from remnant holdfasts or via recruitment. Such variation might be expected in future studies because recovery is affected in part by proximity of propagule sources (Sousa 1984).

Removal of the dominant species can, however, also result in different species preempting space for long periods. DeWreede (1983) removed *Sargassum muticum* from quadrats in the *S. muticum* zone in British Columbia during the same month in three different years. In two cases, *S. muticum* returned to its generally high (approximately 80%) surrounding cover within a few months, while in the third case *Rhodomela larix* rapidly colonized and remained dominant during 4 years of observation. DeWreede (1983) suggested that the colonization of *R. larix* was favored by the coincidence of available space in a year when few *S. muticum* propagules were available.

Recovery after partial clearing may also vary in space, as Dayton (1975) found for *Hedophyllum sessile*. This kelp and its obligate understory recovered to preclearing abundance in 2 years at one site, while it had not recovered after 4 years at another, more sheltered site. Turner (1983*b*) also found that the recovery process after removal of *Phyllospadix scouleri* varied significantly within a site depending on season of removal and other unknown factors.

The above are examples in which late successional species—the generally common, large organisms that typify particular intertidal assemblages—were removed. To date, only Sousa (1979*a*) has examined the effects of removing early or mid-successional species. By definition, these species do not necessarily "recover" when disturbed as they are not the late successional dominants. At Sousa's (1979*a*) site near Santa Barbara, *Ulva* spp. was the common early successional species, *Gigartina leptorhynchos, Rhodoglossum affine,* and *Gelidium coulteri* the middle species, and *G. canaliculata* the late successional species. Removal of *Ulva* resulted in an increase in the abundance of the middle and late successional species, and removal of the middle species resulted in an increase in the abundance of *G. canaliculata.* This indicates that these species inhibit rather than enhance recovery of the late successional dominants characteristic of this zone, and that natural disturbances to these species have significant impacts on subsequent patterns of recovery.

Sousa (1979*a*) also found that herbivores, particularly the crab *Pachygrapsus crassipes,* increased the recovery rate of *G. canaliculata* by preferentially eating *Ulva* spp. Similar effects of herbivores on succession have been found by Lubchenco (1983) in the northeastern United States. In contrast, Foster (1982) found that limpets retarded the recovery of *Iridaea flaccida* in the *I. flaccida* assemblage. However, this alga was among the first, and was the most abundant macroalga, to colonize after clearing.

In the high intertidal and splash zone, limpets may completely eliminate the dominant but visually ephemeral macroalgae during times when conditions for algal growth are poor, producing a regular seasonal succession (Cubit 1984). In the low intertidal and tide pools, selective removal of patches of sea urchins (*Strongylocentrotus purpuratus*) within areas otherwise dominated by macroalgae generally results in colonization by macroalgae (Paine and Vadas 1969; Dayton 1975; Sousa et al. 1981; Gaines 1985). There are no published accounts concerning the recovery rates of sea urchins in these former sea urchin patches.

B. Natural Disturbance

A number of natural biological and physical disturbances have been identified in rocky intertidal communities. Biological disturbances such as predation by starfish on mussels (Harger and Landenberger 1971), by gastropods on mussels and barnacles (Connell 1970; Lubchenco and Menge 1978), and by sea otters on a variety of intertidal animals (Palmisano 1983) have been shown to affect intertidal community structure significantly. Harbor seals also disturb the intertidal zone by hauling out and perhaps by nutrient enrichment (Boal 1980). Grazers such as sea urchins can completely alter local community structure (see Section IV.A.2. above; Lawrence 1975), urchins and crabs may affect recovery rates from other disturbances (Sousa 1979*a*, 1980), and limpets can cause a seasonal succession in the high intertidal (Castenholz 1961; Cubit 1984). However, such biological disturbances are often diffuse and continuous. Thus, these types of disturbances have been studied primarily with experiments involving removals or exclusions that document only the effects of natural densities versus complete absence. We know little about disturbance effects of these species relative to natural variation in their densities and activities. Lubchenco (1978) and

Lubchenco and Gaines (1981) pointed out that grazers may have variable effects depending on their densities, food preferences, and food availability, and studies such as that of Underwood and Jernakoff (1981) using a variety of grazer densities would lend further insight into the natural effects of these animals.

Physical disturbances have received much recent attention, especially along the exposed coast of the northeastern Pacific, and we are beginning to gain a better appreciation of the importance of these phenomena to community structure. Dayton (1971) was the first to try to quantify physical disturbance by logs in Washington state, and found that a point in the intertidal zone had a 5–30% probability of being struck by a log in 3 years. Paine and Levin (1981) estimated that between 0.4 and 5.4% of the mussels on an exposed island in Washington are removed during each winter month by wave action. Dethier (1984) estimated that tide pools in her Washington study areas were disturbed once every 18–20 months. These estimates suggest that rocky intertidal assemblages are dynamic, and that much of the patchiness within an assemblage reflects variation in recovery from prior disturbances (Sousa 1985).

Perhaps the best documented effects of physical disturbance are in mussel beds where waves remove patches of various sizes (Paine and Levin 1981), and where much of the patchiness in the community at any one time does reflect differences in recovery (Sousa 1984). Dethier (1984) studied the effects of various physical and biological disturbances on the species composition and recovery of tide pool assemblages. As suggested by the information from experimental clearings discussed above, she found that the more common partial clearings recover much faster than total clearings. She concluded that disturbance is the major stochastic process generating variability in tide pools.

Earlier species in a particular successional sequence may affect later succession (Sousa 1979*a*), and these species may also have variable responses to disturbance. Sousa (1980) mimicked natural disturbance from waves on various successional stages in an intertidal boulder field by overturning boulders with varying species composition for different lengths of time. He found that early successional species suffered more damage from any particular length of disturbance, but that these species also recovered more quickly. The responses of different species were related to their life history characteristics, especially spore production, dispersal, and ability to grow from remnant holdfasts. This is in agreement with information from experimental clearings, and further indicates the importance of knowing both the disturbance regime and the biology of the species involved to understand the recovery process.

Sand movement also disturbs rocky intertidal communities (Daly and Mathieson 1977; Mathieson 1982; Taylor and Littler 1982; Littler et al. 1983; Turner 1983*b*), reduces herbivore densities (Robles 1982), and can set the lower boundaries of distribution of certain species (Frank 1965; Daly and Mathieson 1977; Littler et al. 1983; Section III). In areas where sand movements are seasonal, burial often kills ephemeral species (e.g., *Chaetomorpha linum, Ulva lobata, Chthamalus dalli*) that later resettle when sand moves offshore (Daly and Mathieson 1977; Littler et al. 1983). The resulting seasonal succession is thus similar to that caused by limpets in the high intertidal. Rocky habitats regularly disturbed by sand are also usually inhabited by a few perennial species, such as *Anthopleura elegantissima, Phyllospadix scouleri* (see Littler et al. 1983), *Gymnogongrus linearis* (see Markham and Newroth 1972), *Laminaria sinclarii* (see Markham 1973), *Rhodomela larix* (see D'Antonio 1986), and algal turfs (Stewart 1983) that can tolerate abrasion and burial.

Perhaps the most pervasive physical disturbance other than wave shock is that produced when extremely hot weather coincides with low tides. Most investigators making regular visits to the shore have observed the general "bleaching" of seaweeds resulting from such conditions. To our knowledge, neither such disturbance nor later recovery has ever been quantitatively examined, but most of the algae appear to rapidly produce new blades from undamaged basal and holdfast tissue (M. S. Foster, pers. obs.). A similar bleaching may result from freshwater runoff. Extreme cold may cause loss of limpets by exfoliation of rock (Frank 1965) and damage to various organisms in tide pools (Dethier 1984).

Changes in weather conditions may also indirectly affect intertidal organisms by encouraging disease outbreaks. Dungan et al. (1982) describe a "catastrophic" decline of a predatory sea star in the Gulf of Mexico, a decline caused by a disease associated with a prolonged period of elevated temperatures. The consequences of this decline were not documented.

Landslides and elevation changes resulting from earthquakes and nuclear testing are examples of extreme physical disturbances. There are no published observations of recovery after landslides in the rocky intertidal of the northeastern Pacific, but such observations would be a valuable contribution to our knowledge of succession because subsequent "recovery" would have to be solely from new settlement. Uplifting from the 1964 Alaska earthquake and the 1969 "Milrow" nuclear test caused a die-off of most species whose elevation was raised. These species were replaced by others that generally occur higher in the intertidal zone than those originally present (Haven 1972; Johansen 1972; Lebednik 1973).

These studies all suggest that a variety of disturbances affect rocky intertidal communities. The types, severity, and frequency of disturbance on mussel beds, boulder fields, and tide pools at selected sites have been documented, and related to within-zone patterns of distribution and abundance. However, similar studies in the same habitats at different sites are needed to determine the general importance of these events. This is especially necessary because we know that changes resulting from storms vary with site (discussed in Sections II and III). Moreover, with the exception of Dayton (1975) and Sousa (1979*a*), there are no studies of the importance of the disturbance process in assemblages dominated by perennial macroalgae (e.g., *Endocladia muricata, Iridaea flaccida*) in the northeastern Pacific. In Chile, Jara and Moreno (1984) studied the structure of a mid-intertidal assemblage composed of a mosaic of areas dominated by either *Iridaea boryana* or barnacles and crustose algae. The structure of the assemblages depended upon the occurrence of various disturbance agents that created free space within the community. Depending upon the time of year and local herbivore abundance, two different ensuing successional sequences occurred. Thus, at any given time the spatial variation in this community is due to three interrelated factors: bare space created by disturbance, different successional sequences initiated by the disturbance, and the phase of succession at the time of observation. Similar studies of ubiquitous perennial macroalgal assemblages in other temperate areas would aid in determining the degree

to which we can generalize about the importance of disturbance, particularly physical disturbance, in structuring rocky intertidal communities.

V. Effects of Disturbance Caused by Humans

Pollutants discharged by humans may cause alterations in distribution, abundance, and composition of rocky intertidal communities. However, they differ in important ways from natural factors that may cause similar changes (Auerbach 1981). Wastes discharged to the ocean typically emanate from point sources, and result in gradients of change that decrease with distance from the source (e.g., municipal wastes). These wastes are often composed of complex, variable mixtures of toxic substances, and are discharged almost continuously. Nonpoint sources of wastes also enter coastal waters (e.g., storm runoff), as do pollutants transported by rivers and streams.

Our understanding of the effects of each of these different modes of discharge differs greatly with ability to sample the input adequately, and to detect and interpret ecological effects. The types of wastes or disturbances considered in this review include: petroleum hydrocarbons, chemical dispersants, municipal wastes, pulp mill effluent, and recreational uses. These types were selected because: (1) there was demonstrated evidence of direct impacts on rocky intertidal communities, (2) insight could be gained even if evidence of effects was observed in other habitats, (3) potential for impacts along the California coast was likely to continue or increase, and (4) evidence of community degradation or recovery was clearly linked to presence of waste discharge.

This review is not exhaustive, particularly for petroleum hydrocarbons. Although the literature on ecological effects of pollution is voluminous, the literature on these types of wastes is extremely uneven, and this is reflected in our level of treatment. Nevertheless, much has been learned about the structure, behavior, and composition of marine communities as a result of studies of changes in communities due to pollution, particularly from point source effluents. Unfortunately, there has been a strong tendency to focus attention on catastrophic acute effects, like oil spills, rather than to examine the low-level impacts from chronic input. Therefore, the quantity of information does not necessarily reflect the seriousness of potential ecological effects for a particular waste type.

A. Petroleum Hydrocarbons

The scientific literature on oil spills is exceptionally large, but generally anecdotal. It is based on short-term studies and syntheses of postaccident observations. Results from different oil spills are not readily comparable, certain habitats are emphasized (e.g., rocky intertidal) while others are often omitted (e.g., subtidal), only catastrophic effects are usually studied and, other than conjecture about habitat sensitivity, few predictions are possible.

Each spill is unique because numerous variables affect spill impact. These include type of spill, duration of exposure, volume and type of oil, oil state and age (degree of weathering), hydrographic conditions, weather, season, biological environment, use of dispersants, etc. (Straughan 1972; BNCOR 1980). It is also difficult to generalize because of our limited understanding of the structure and functioning of marine communities and our limited ability to sample these communities quantitatively and interpret changes. Nonetheless, it is clear that oil pollution may cause mortality directly through coating and asphyxiation, contact or ingestion, exposure to toxic fractions, impacts on sensitive early life stages, and through disruption of insulation properties of birds and mammals (Boesch and Hershner 1974). Mortality may also be caused in more subtle ways such as disruption of feeding, lowered resistance to stress, uptake of carcinogenic or mutagenic constituents, impaired reproduction, and altered behavior.

The study of accidental oil spills can yield important qualitative information about cause and effect relationships (Moore and McLaughlin 1978). However, long-term effects are poorly understood and long-term studies have focused on single habitats and selected species. Consequently, generalized statements regarding community recovery are not possible (see reviews in Boesch and Hershner 1974; Baker 1976, 1983; BNCOR 1980; Johnston 1984; Teal and Howarth 1984).

Although several oil spills on the west coast received considerable scientific attention, much of our understanding of oil spill impacts comes from studies of spills on other coasts. Of the hundreds of spills reported over the last 25 years throughout the world, about 50 are discussed in the literature, and only a dozen or so of these have been studied in depth. These include the spills listed in Table 6, which are discussed by NAS (1975), Teal and Howarth (1984), and Johnston (1984).

1. Sources

Although catastrophic oil spills are some of the most conspicuous forms of marine pollution, they are not the major contributors of hydrocarbons to the ocean. Significantly greater quantities are contributed by terrestrial runoff, discharge of municipal wastes, aerial fallout, natural seeps, tanker operations, and refineries. These inputs are, however, inconspicuous, poorly monitored, and inadequately quantified. General estimates of worldwide input from these sources have been made by numerous authors (i.e., NAS 1975; Hardy et al. 1977; Mileykovskiy 1979; Wardley-Smith 1979; Johnston 1984). Detailed discussions of global inputs have been published by Clark and Macleod (1977) and Grossling (1976) and U.S. inputs are reviewed by the NAS (1975, 1985) and by Boyd et al. (1976). In 1975 the NAS estimated that acute tanker spills (1,373,832 barrels) accounted for only 3.3% of the total annual hydrocarbon input of 42,057,440 barrels, while tanker operations, such as bilges bunkering, dry docking, load-on-top and non-load-on-top tankers, etc. (13,278,084 barrels), accounted for 31.6%. In 1985 the NAS estimated that the total annual input of petroleum hydrocarbons to the marine environment ranged from 11,696,000 barrels to 60,544,000 barrels. Acute tanker spills (2,064,000–2,752,000 barrels) accounted for 4.6–17.7% of the total input, while tanker operations accounted for 23.9–35.3% (4,128,000–14,448,000 barrels) of the total.

The nearshore waters of the northeastern Pacific receive petroleum hydrocarbons from all of these sources. Data on input to this region, however, are incomplete and estimates have been made for only a few categories. Even though their overall input is relatively small, the ecological effects that can result from catastrophic spills has generated concern for similar potential disasters along the California coast. For example, tanker traffic

TABLE 6. EXAMPLES OF WELL-DOCUMENTED MAJOR OIL SPILLS.

Date (day/mo/yr)	Oil source	Impact location	Volume spilled (barrels)*	References
29/03/57	*Tampico Maru*	Baja California, Mexico	60,000	North et al. (1965)
13/01/67	*Chryssi P. Goulandris*	Milford Haven, England	860,000	Nelson-Smith (1968)
18/03/67	*Torrey Canyon*	Cornwall, England	804,960	Smith (1968)
16/09/69	*Florida*	West Falmouth, Massachusetts	4,500	Blumer and Sass (1972)
28/01/69	Platform A	Santa Barbara, California	75,561–769,346	Foster et al. (1971*a, b*)
04/02/70	*Arrow*	Chedabucto Bay, Nova Scotia, Canada	108,000	Thomas (1973)
18/01/71	*Arizona Standard & Oregon Standard*	San Francisco Bay, California	20,000	Chan (1973)
09/08/74	*Metula*	Strait of Magellan, Chile	357,760	Baker et al. (1976)
15/12/76	*Argo Merchant*	Nantucket, Massachusetts	192,640	Pollack and Stolzenbach (1978)
22/04/77	Platform Bravo	Ekofisk Field, North Sea	137,600	Teal and Howarth (1984)
26/10/77	*Tsesis*	Baltic Sea	7,568	Kineman et al. (1980)
16/03/78	*Amoco Cadiz*	Portsall, France	1,720,000	Hess (1978)
03/06/79	IXTOC 1	Bahia de Campeche, Mexico	3,000,000–10,000,000	Teal and Howarth (1984)

* One barrel = 42 gallons (U.S. liquid) = 321 pounds.

to the Ports of Los Angeles/Long Beach is expected to double by 1991 (J. Boyd, pers. comm.). Since the number of tanker accidents is correlated with the volume of oil produced and the amount of tanker traffic (Beyer and Painter 1977; Goldberg et al. 1981; Meade et al. 1983), catastrophic oil spills are expected to occur with increasing frequency in the future. Beyer and Painter (1977) analyzed data on worldwide tanker spills during 1969–72 and found that the average frequency of tanker accidents was positively correlated with proximity to harbors, number of port calls (0.92 spills/10^3 port calls), volume transported (12 spills/10^9 barrels transported), and vessel age (20 spills/10^3 vessel years), and negatively correlated with vessel size. Although the average spill was about 7,100 barrels, use of this statistic can be misleading for spills that result in ecological damage. For example, the NAS (1975) reported that while 98% (3,468 spills) of the spills in the U.S. (totaling 17,200 barrels) were each less than 220 barrels, four spills accounted for 65% (221,536 barrels) of the volume lost during 1970. Such analyses of worldwide data are useful because they basically corroborate trends observed in the northeastern Pacific. Although California offshore production is expected to increase over six times from 80,000 barrels to 500,000 barrels per day (J. Boyd, pers. comm.) by 1991, most of this oil may be transported by subsea pipelines.

According to the U.S. Goast Guard's Pollution Incidents Reporting System (PIRS), a total of 335 spills were reported between San Diego and the Strait of Juan de Fuca from 1973 to 1984, representing a volume of 43,883 gallons. Eighty-eight percent of this volume (38,518 gal) was lost from vessels and 12.1% (5,267 gal) from coastal marine facilities. Most of the vessel spills were either distillates (150 spills, 20,687 gal) or crude oil (24 spills, 11,406 gal). Unfortunately, the PIRS includes only spills from vessel accidents caused by collision, grounding, ramming, fire, or explosion, and only operational spills associated with refueling, and loading or unloading cargo. Reliable estimates of input from deballasting, bilge pumping, and tank cleaning are not available.

The majority of vessel spills occurred along the Olympic Peninsula (37.4%), in San Francisco Bay (30.3%), and in the Los Angeles/Long Beach harbor area (17.5%). A total of 12,333 gal was spilled from 58 individual vessels between Point Conception and Crescent City. The majority of spills from marine facilities occurred along the Olympic Peninsula (15.4%), Point Arena (75.9%), and the Los Angeles/Long Beach harbor area (45.1%). A total of 1,765 gal were spilled from eight marine facility incidents within the Point Conception–Crescent City area. Between 1973 and 1983 there has been an average of 30 spills per year in the region.

Spill records are poor prior to 1973, so the above data exclude a number of major oil spills including the collision of the *Arizona Standard* and the *Oregon Standard* (Table 6), the blowout of Platform A off Santa Barbara (Table 6), the *Yukon* in Cook Inlet (5,000 barrels), a barge near Anacortes, Washington (5,000 barrels), the *Manatee* off San Clemente, California (29 barrels), the *Private Joseph Merrell* off Monterey, California (381 barrels), as well as a pipeline break in Bellingham, Washington (11,905 barrels), and a tank valve failure in Oakland, California (4,167 barrels).

2. BIOLOGICAL EFFECTS

Much is known about the acute effects of large catastrophic oil spills on rocky intertidal communities (see reviews by Hardy et al. 1977; Clark 1982*a, b*; Baker 1983; Johnston 1984; Teal and Howarth 1984). However, little is known about long-term effects or recovery processes (Clark 1982*b*), and even less about the effects of low-level inputs (Hardy et al. 1977). Field analyses are hampered by the lack of controls and inherent population variability (Michael 1977; Mann and Clark 1978; Teal and Howarth 1984).

Van Gelder-Ottway (1976), NAS (1975), and Johnson and Pastorok (1982) compiled lists of the major world oil spills for which rocky intertidal impacts have been documented. Of these 30 or so spills, relatively few occurred on the west coast of the United States. These include the *Tampico Maru* (1957) wreck off Baja California, Mexico, the Santa Barbara blowout at Platform A (1969), the collision of the *Arizona Standard* and the *Oregon Standard* (1971) at the entrance to San Francisco Bay, the wreck of *General M. C. Meigs* (1972) in Washington, the wreck of the *Irish Stardust* in British Columbia (1973), the wreck of a barge in Anacortes, Washington (1971), and more recently, the explosion of the *Puerto Rican* (1984) off San Francisco Bay. Each of these spills proved to be unique, and impacts differed markedly.

Clark et al. (1973, 1978) investigated the effects of the wreck

of the *General M. C. Meigs* on the rock intertidal community near Cape Flattery, Washington, and compared disturbed areas to an unoiled control site 6.4 km to the north. Initial oil-related loss was relatively small. Blade loss in *Laminaria setchellii* and *Phyllospadix scouleri* was evident, as was bleaching of *Corallina vancouveriensis, Prionitis lanceolata,* and *Ceramium* sp. There were no gross impacts on sessile animals (e.g., barnacles, mussels and anemones). Dead and abnormal (i.e., spine loss) *Strongylocentrotus purpuratus* were found. Tissue analyses suggested that bioaccumulation of petroleum hydrocarbons occurred in *Fucus gardneri, Pollicipes polymerus,* and *Hemigrapsus nudus.* Long-term monitoring after the accident indicated continued impacts of the spill on urchins, barnacles, mussels, and anemones, as well as continued bioaccumulation. *Hedophyllum sessile* became the dominant alga after 1½ years. After 2½ years the cover of the algae *Halosaccion glandiforme, Egregia menziesii, Desmarestia* sp., *Mastocarpus papillatus, Rhodoglossum affine, Iridaea* sp., *Codium fragile,* and *Ulva lactuca* returned to "normal."

Cretney et al. (1978) made successive observations of the impact of 200 tons of spilled fuel oil on an isolated and sheltered rocky cove on Vancouver Island, British Columbia, following the wreck of the *Irish Stardust.* Initial biological effects occurred over 9 months and included loss of heavily oiled *Fucus distichus* and mortality of limpets, amphipods (*Orchestia* sp.), and periwinkles (*Littorina* spp.). Presence and degradation of various oil fractions from stranded oil patches were documented over a 4-year period, even though most organisms had "recovered" within a year.

Chan (1973) reported a significant decrease in marine life at Sausalito and Duxbury Reef near San Francisco as a result of the collision of the *Arizona Standard* and the *Oregon Standard.* Disturbances attributed to smothering were patchy as the oil stranded unevenly throughout the upper rocky intertidal zone. Chan was able to resample specific prespill study sites, and found significant mortality in *Balanus glandula, Chthamalus* sp., *Mytilus californianus, Collisella digitalis, Collisella scabra, Littorina scutulata/plena, Tegula funebralis, Pollicipes polymerus,* and *Pachygrapsus crassipes.* Oil residue was still visible 10 months after the spill. Species apparently unaffected by the oil included *Pisaster ochraceus, Lottia gigantea, Aplysiopsis smithi,* rock boring piddocks, *Cancer antennarius,* sea anemones, chitons, *Haliotis rufescens, Endocladia muricata, Halosaccion glandiforme, Iridaea flaccida,* and *Mastocarpus papillatus. Urospora pencilliformis, Porphyra perforata, Enteromorpha intestinalis,* and *Phyllospadix scouleri* increased in abundance after the spill.

Chan (1975) followed the effects of the spill from this collision for 39 months. Less than 5% of the original oil residue remained on rock surfaces at the end of the study. Significant recruitment was observed for barnacles, mussels, periwinkles, limpets, and algae. Most algae had recovered to prespill densities, and *Urospora pencilliformis* was reduced significantly. Densities of *Tegula funebralis* returned to prespill values within 6 months while limpet densities nearly doubled within 18 months, and then returned to normal at 30 months. Numbers of *Mytilus californianus* doubled within 18 months. *Pachygrapsus crassipes* and *Littorina keenae* had not recovered by the end of the study.

The effects of the wreck of the *Tampico Maru* on a small cove in Baja California were studied qualitatively for 6 years by North et al. (1965). Since no prespill data were available, comparisons were made to adjacent unoiled sites. Initial observations were made about a month after the accident. The authors distinguished several phases of disturbance and recovery, including complete disappearance, immigration and colonization, and maturation. Widespread mortality was obvious in many species (e.g., *Haliotis fulgens, H. rufescens, H. cracherodii, Panulirus interruptus, Tivela stultorum, Mytilus* spp., *Strongylocentrotus franciscanus, S. purpuratus, Pisaster giganteus,* and *P. ochraceus*). Survivors included *Littorina keenae, Anthopleura xanthogrammica, A. elegantissima,* and *Corynactis californica.* Within 4 months immigration of mobile species was evident (e.g., fish, *P. interruptus, Aplysia californica, Pisaster* spp., *Pachygrapsus crassipes*) as well as some colonization (e.g., *Mytilus* spp., *Chthamalus* spp., *Patiria miniata*). Extensive recovery had occurred after 31 months. The authors assumed that severe damage to algae had occurred since there were few attached plants on the shore. Within 3 months, rapid algal colonization had occurred both intertidally and subtidally, and included *Macrocystis pyrifera, Cystoseira osmundacea, Halidrys dioica, Porphyra perforata, Egregia menziesii, Iridaea* sp., and *Ulva lactuca.* Rapid algal colonization was attributed to high toxic thresholds, reduction of grazer and filter feeder densities, and wave protection afforded by the sunken vessel. Long-term changes included development of the kelp forest and continued slow recovery of sea urchins, mussels, and abalones.

Because of their potential for release of significant quantities of oil, offshore oil platforms are of major concern. The blowout of Platform A 9.7 km offshore in the Santa Barbara Channel was one of the first platform spills of major size. Its effects proved difficult to evaluate, and caused considerable controversy (Neushul 1972). Much of the heavy crude oil underwent considerable weathering prior to stranding on shores (Straughan 1971). The oil was unevenly distributed along the coast over a distance of 161 km and persisted as asphaltic patches on upper intertidal rocky surfaces in some locations for at least 7 months (Nicholson 1972). The spill also coincided with severe winter storms, coastal runoff, and turbidity (Straughan 1971). In fact, Cimberg et al. (1973) concluded that at some sites sand movement and substrate stability were more important in affecting presence of intertidal organisms than was presence of oil. Observed impacts were difficult to interpret in the absence of measures of prespill conditions and meaningful reference sites (Neushul 1972; Foster and Holmes 1977). Moreover, estimates of input along the shore ranging from 2.7 to 118.1 metric tons/km indicated extreme variability in shore exposure (Foster et al. 1971*a*). The presence of kelp forests may have protected some rocky shores (Neushul 1972). Damage was reported by numerous authors (e.g., Battelle Northwest 1969; Foster et al. 1971*b*; Nicholson and Cimberg 1971). However, Foster and Holmes (1977) concluded that it was impossible to make any more than very gross quantitative estimates of overall mortality, and inferences about recovery could only be qualitative for a few species. Significant, widespread impact was reported only for *Phyllospadix torreyi* and *Chthamalus fissus* (Foster et al. 1971*b*). Although 16 other algal species were clearly damaged by oil, it was not possible to interpret the overall level of impact. Mortality was also reported for *Notoacmaea paleacea, Mytilus* spp., *Pugettia producta, Pagurus* spp., *Idotea* spp., *Pollicipes polymerus, Enteromorpha* spp., *Ulva* spp., *Porphyra* spp., *Gigartina* spp., and *Hesperophycus harveyanus* (Straughan 1971; Foster and Holmes 1977).

Other than the common loss of grazers followed by algal blooms, it is difficult to generalize about these spills, or to make specific statements about effects that might be anticipated should a new major oil spill occur in the region. Even a cause–effect relationship between grazer loss and algal blooms is questionable as blooms could also result from mortality of competitors. Analyses of oil spills that were studied in depth at a few sites yield evidence about the local nature of oil spill effects, but provide little comprehensive information about possible widespread significance of these effects. These studies may or may not be able to detect sublethal or long-term effects. Conversely, impact assessment studies designed to yield information about extent of the overall impacts, e.g., total number of acres of kelp lost or number of birds killed, have not yielded information concerning altered community structure and perhaps function, or provided a basis upon which to make statements concerning recovery. These studies may only enable detection of catastrophic impacts, even though not all spills cause catastrophic impacts. To complicate the situation further, Nicholson (1972) pointed out that rocky intertidal populations in southern California, particularly those in the upper intertidal, may have already been stressed by years of chronic pollution, causing an increase in ephemeral plants (e.g., *Ulva* spp., *Enteromorpha* spp., diatom films, and small green algal turfs), and a decrease in slow-growing perennials such as *Endocladia muricata, Pelvetia fastigiata,* and *Hesperophycus harveyanus.*

3. Oil Spill Experiments

Despite a very thorough and convincing argument by Moore and McLaughlin (1978) in favor of intertidal oiling experiments, there have been very few such experiments in rocky intertidal communities. Moreover, dosing protocols have varied considerably to suit different study objectives. Dosing has been done by spraying oil at sites during low tide, followed by additional oil applications during successive tides and/or use of dispersants, or by application of oil to the water overlying the intertidal zone during high tide. In fact, Moore and McLaughlin (1978) were not optimistic about obtaining realistic information from such experiments because of the practical difficulties of using oil as a dose treatment adjacent to a control, and because of the compromises in experimental design that must be made due to the inherent heterogeneity of the habitat.

Crapp (1971) observed reductions in densities of pure stands of *Semibalanus balanoides* and *Chthamalus stellatus* at Stackpole Quay following a 6-hour dose of Kuwait crude oil (100%?) applied directly during low tide. No impact was noted in a second experiment at Greenala Point using an undiluted crude oil dose of 2 liters/m^2. In a third experiment, atmospheric residues of the same oil caused physical dislodgement of littorines and topshells, producing a greater impact than did Kuwait crude oil applied directly. The latter was apparently readily removed by tidal action.

Nelson (1982) conducted a series of comprehensive quantitative oil experiments in a Norwegian fjord using weathered Ekofisk crude oil to examine the effects of dose level and duration, test site exposure, and seasonality on the cover of intertidal organisms. Random point sampling was used to estimate changes in area occupied by each species and the area covered by algal canopy before and from 4 to 51 days after oiling at low tide. The major species of interest were *Semibalanus balanoides, Mytilus edulis, Patella vulgata, Fucus vesiculosus, Cladophora rupestris, Ascophyllum nodosum, Gigartina stellata,* as well as isopods (*Jaera albifrons, Idotea pelagica*), an amphipod (*Hyale nilssoni*), gastropods (*Nucella lapillus, Littorina* spp.), and *Spirorbis corallinae.* No changes were found at doses of 0.2 and 2.0 liters/m^2. An increase in cover of *Mytilus edulis* (by immigration of adults?) at the multiple dose site 8 days after oiling was the only significant change observed with change in dose frequency. Decreases in cover of *Gigartina stellata* and *Fucus vesiculosus* and abundance of *Littorina* spp. were noted at protected sites, but not at exposed sites. Nelson (1982) concluded that few gross negative impacts of oiling were observed on adult organisms. Increases were attributed to seasonal changes in biological activity. *Semibalanus balanoides, M. edulis,* and *F. vesiculosus* adults appeared to be highly resistant to oiling, while juveniles were sensitive. In the future it would be beneficial to study the effects of oiling on reproduction and recruitment, in addition to changes in existing community structure.

Bonsdorff (1983) studied effects of Ekofisk crude oil on tide pools near Bergen, Norway. Significant mortality of the invertebrate community inhabiting *Corallina officinalis* (ostracods, harpacticoids, and amphipods) occurred, followed by recovery in less than a month. *Patella vulgata* accumulated aromatic hydrocarbons tenfold and then depurated to normal within 38 days.

Other workers have used artificial substrata or done transplant studies to examine recovery of intertidal communities from oil spills. As part of a larger experimental oiling study in the Strait of Juan de Fuca, Vanderhorst et al. (1980) studied epifaunal recruitment and the survival of limpets on experimentally oiled bricks. Oil significantly reduced recruitment density and species richness. Detritivores were insensitive to oil treatment while limpets and suspension feeders were very sensitive. Although most of the oil (84%) was leached from the bricks within 5 days, the residual oil was sufficient to significantly inhibit recovery. After observing barnacle settlement on weathered, oiled surfaces in the field, Straughan (1971) studied barnacle recruitment to oiled and unoiled settling plates. Recruitment to oiled plates increased with oil weathering, and also varied with tidal level due to thermal effects.

Few predictions have emerged from studies of past oil spill effects. Field experiments have greater predictive potential as various treatment effects can be rigorously evaluated. We conclude that greater emphasis should be given to experimental field studies, even though "dosing" methodology represents a significant design obstacle.

B. Oil Dispersants

Chemical oil treatment agents (e.g., dispersants, emulsifiers, detergents) have been included in this review because of their high potential for use in "control" of oil spills at sea or as a "cleanup" method for removing stranded oil on the shore.

Despite a large, well-reviewed literature (e.g., IPIECA 1980; Nelson-Smith 1980; McAuliff 1984), our understanding of ecological impacts of dispersants is still very limited, variable in quality, and controversial (NAS 1975; Johnson and Pastorok 1982; Sprague et al. 1982). In effect, obvious acute oil spill impacts are traded for less obvious perhaps sublethal impacts,

as dispersed oil penetrates a greater range of habitats and organisms (Sprague et al. 1982). The ecological consequences of dispersing oil at sea have been almost impossible to document, and predicting field effects from laboratory studies intended for ranking dispersant effectiveness has not been fruitful. Information obtained from studies of actual oil spills where dispersants were used has provided the most insight into ecological effects. Unfortunately, much of this information is based upon qualitative estimates of changes in abundance of species, presence/absence of species, or observations about "biological condition." It has also been difficult to compare impacts from different spills because of confounding differences in oil composition, spill conditions, and variation in habitat attributes. Perhaps the most insight has come from actual field experiments in intertidal environments, even though these are difficult to do because of problems associated with handling or containing specific dose treatments and in defining and locating treatment and control replicates.

1. Impact of Dispersants Applied to Spills

The ecological impacts of use of chemical oil spill cleanup agents to remove stranded oil from rocky shores have been well summarized by Nelson-Smith (1968, 1978), Crapp (1971), Cowell (1978), and by Johnston (1984). Impacts vary with dispersant type, frequency and quantity used, type of shore and exposure, season, species sensitivity, sampling ability, and from acute to more subtle delayed effects, e.g., changes in growth. Use of dispersants in the field enhances the potential toxicity of crude oil (BNCOR 1980), especially in sheltered habitats on shore (Sprague et al. 1982). In cases where densities of algal grazers or sedentary filter feeders (e.g., mussels, barnacles) were reduced, dramatic changes in assemblage structure, dominants, and distribution have been reported. Crapp (1971) found that emulsifiers reduced or eliminated many dominant animal species which permitted invasion and dominance by green and brown algae, resettlement of grazers, and potential recovery over an extended period of time. This apparent settlement and unchecked growth of algae has been documented several times as a result of shore cleaning, but also has been reported as a consequence of natural perturbations (Southward and Southward 1978; Section IV). However, Crapp (1971) pointed out that little information was available for evaluating impacts on species other than conspicuous dominant forms. Cowell (1978) reported that use of dispersants near shore does not have a measurable effect on commercial fisheries offshore.

2. Dispersant Experiments

a. Laboratory

There is an extensive literature on the acute toxicity response of numerous marine species to various oil dispersant chemicals tested in the laboratory. More recently, sublethal effects on growth, respiration, and biochemistry have been reported. Much of this literature has been reviewed by Beynon and Cowell (1974), McCarthy et al. (1978), and Swedmark et al. (1971, 1973). There has also been interest in standardizing test procedures to facilitate comparisons of toxicity and effectiveness among dispersants (Hazel et al. 1970; Laroche et al. 1970; Tarzwell 1971; Baker and Crapp 1974; Bellan 1974; Cowell 1974; Gunkel 1974; Swedmark 1974; Wilson 1974; Wilson et al. 1974; Doe and Wells 1978; Norton et al. 1978; Lewis and Suprenant 1983). This has enabled development of less toxic dispersants which are now being actively reconsidered as a preemptive control method offshore (NAS 1975; Wardley-Smith 1983). However, by formalizing test procedures and selecting standardized test species, simulation of actual field conditions is often ignored and ecological predictions of effects have become difficult if not impossible (Baker and Crapp 1974; Cowell 1974; Wilson et al. 1974; Grassle et al. 1981).

b. Field

The general lack of data on prespill conditions has compromised the usefulness of much of the information gathered from studying effects of actual oil spills in which dispersants have been used (Cross and Thomson 1982). Such studies have also been generally deficient in supportive oceanographic, atmospheric, and water column hydrocarbon concentration data.

Bryan (1969) reported on the range of impacts of various detergent treatments on populations of the dogwhelk *Nucella lapillus* following oiling of the rocky shores on Porthlevon, Cornwall from the wreck of the *Torrey Canyon.* Dogwhelk populations clearly declined with increased use of detergent. At "sublethal" levels, growth was affected as evidenced by shell markings. Based on counts, Crapp (1971) found greater mortality of midlittoral barnacles (*Semibalanus balanoides* and *Chthamalus stellatus*) exposed during low tide to sequentially applied oil and dispersant than of barnacles exposed to only oil. *Littorina neritoides, L. saxatilis, Mytilus edulis, Patella vulgata,* and *N. lapillus* were also more sensitive to oil and dispersant treatments than to oil alone. Battershill and Berquist (1982) reported that both dispersed fresh and weathered oil were more toxic to caged intertidal gastropods (*Nerita atramentosa*), dosed at low tide, than were the same oils untreated with dispersants.

In an attempt to compare differences in effects of oil alone and oil treated with modern dispersants, Crothers (1983) compared oil only, dispersant only, and combined oil–dispersant treatments on fixed quadrats in winter and summer on a midlittoral rocky shore in West Somerset, England. There were no changes in densities of lichens or mussels (*Mytilus edulis*) and no changes or only slight reductions in barnacle (*Chthamalus* spp., *Semibalanus balanoides, Elminius modestus*) densities in oil or oil plus dispersant treatments. Neither *Littorina littorea* nor *L. saxatilis* were affected. Density of limpets (*Patella vulgata*) was significantly reduced by both oil and oil plus dispersant treatments, but not by the dispersant alone. Subsequent cover by *Fucus* sp. seemed to vary with the number of limpets and with the amount of initial cover prior to treatment. Impacts were greater during winter and recovery was slower.

Preliminary results reported by Blackall and Sergy (1983) on an experimental oil spill on Baffin Island indicate that while dispersants appear to enhance immediate littoral and sublittoral effects, the organisms may be able to survive and recover from such short-term, high-level exposures. Marked mortality of benthic organisms was observed subtidally at depths of 3 and 7 m at dispersed oil test sites. Oil alone has some impact on littoral amphipods and some larval fish, on the density of sublittoral sea urchins, and growth of *Macoma calcarea.* The authors felt that they may have underestimated impacts by conducting the

first postspill survey too soon. In a subsequent study, Boehm et al. (1984) indicated that both treated and untreated oil that had been incorporated into the beaches continued to be a chronic source of oil, as evidenced by bioaccumulation in *M. calcarea* and *Strongylocentrotus droebachiensis.*

In a series of field and laboratory experiments, Rowland et al. (1981) showed that dispersants increase penetration of oil into and movement within intertidal sediments. Consequently, sand beaches may be assumed to function as a potential reservoir of accumulated petroleum, thereby prolonging oil exposure to any adjacent rocky intertidal habitats.

3. Recolonization after Application of Dispersants

Straughan (1971) did a simple field colonization experiment to determine the differential effects of oil, oil plus detergent, or no oil on settlement of *Chthamalus fissus* on treated asbestos plates. She concluded that larvae settled in greater numbers on plates treated with oil and oil plus detergent due to the absence of competing algae and darker color of the plates, suggesting that oiled substrata in the upper intertidal favored settlement of barnacles, while oil cleaning would favor algal colonization.

Documentation and interpretation of recolonization processes of rocky intertidal communities following actual oil spills that were subsequently "cleaned" by use of dispersants has proven to be extremely difficult. Recolonization events following use of dispersants, such as those described by Southward and Southward (1978) for a limpet-dominated shore at Cornwall, are still only predictable in a very general way. Recolonization events described by Southward and Southward (1978) included: (1) development of a diatom film, (2) *Enteromorpha* maximum, (3) maximum *Fucus* cover, replacement of *Enteromorpha,* (4) minimum settlement of barnacles, (5) maximum densities of *Patella* and reduction of *Fucus* settlement by grazing, (6) increase in barnacle settlement and reduction in *Patella,* and (7) stability of the *Patella*–barnacle-dominated assemblage. Other events reported, which varied with exposure, oiling, dispersant use, habitat composition, types of trophic structures, etc., included: (1) changes in vertical ranges of algae in the absence of grazers, (2) changes in vertical ranges of invertebrates benefiting from increased cover of algae, (3) alterations in species interactions, (4) differing time scales of resettlement, (5) changes in recruitment, (6) reduction in number of species, and (7) increase in biomass. Southward and Southward (1978) surmised that in other areas where limpets were less dominant and grazing and predatory systems more complex (such as the Pacific coast of North America), induced disturbance from oiling and use of dispersants could be even more severe.

In the absence of clear definition of terms, "recolonization" (i.e., settlement and growth of recruited organisms) has sometimes been used synonymously with "recovery," i.e., recolonization and succession leading to reestablishment of a community similar in composition to that prior to a pollution event. In the oil literature, this prior community is also often assumed to be "balanced," "normal," "stable," and/or "healthy." Such terms are usually not defined. In attempting to dispel the misconception of rapid and complete recovery that has become established in the literature, Southward and Southward (1978) reiterated the earlier observations of Cowell et al. (1972), who suggested that recovery would be very protracted. In summary, use of dispersants to clean up stranded oil on shore is inadvisable. Their use to control oil spills offshore enhances biodegradation, minimizes bird mortality and fire hazard, "protects" shore habitats, and reduces formation of tarlike residues. However, enhanced toxicity and uptake of oil by pelagic food chains, long-term ecological consequences, degree of spreading, organism uptake, and accelerated deposition are still of concern in offshore applications.

C. Municipal and Pulp Mill Wastes

There is little doubt today that "excessive" discharge of complex municipal wastes into coastal marine environments has resulted in ecological change. Impacts on communities associated with hard substrata may be more transitory than those associated with unconsolidated substrata, where accumulation of organic particulates alters the interstitial environment (Gerlach 1981; Reish 1984). Several studies, however, have reported conspicuous sewage impacts on marine littoral and shallow sublittoral macrophytes. For example, Littler and Murray (1975) studied the impacts of a small, untreated sewage effluent in Wilson Cove, San Clemente Island, California. Intertidal algal assemblages adjacent to the discharge were characterized by reduced community diversity, stratification (spatial heterogeneity), and complexity, and possibly lowered "stability." The macrophytes *Egregia laevigata, Halidrys dioica, Sargassum agardhianum,* and *Phyllospadix torreyi* were replaced by *Ulva californica, Gelidium pusillum, Pterocladia capillacea,* and blue-green algae in the mid-intertidal zone, and by the mollusc *Serpulorbis squamigerus* and *Corallina officinalis* var. *chilensis* in the lower intertidal in the area disturbed by sewage. Results of a clearance experiment designed to measure rates of recolonization indicated that the wastewater plume selected for rapidly growing, opportunistic colonizers, such as *U. lactuca, G. pusillum, P. capillacea,* and blue-green algae, as well as for suspension feeders. The unpolluted control stations were characterized by less productive, morphologically complex macrophytes, high species diversity and abundance, predominance of perennial forms with complex life histories, and greater spatial heterogeneity (i.e., layering). Impacted stations were characterized by opportunistic species with simple life histories, turflike form, low spatial heterogeneity, high production and more macroinvertebrates, and in general an earlier successional stage. The outfall stations exhibited significantly less algal cover and more macroinvertebrates in the lower intertidal, but greater algal cover and fewer macroinvertebrates in the upper intertidal.

Borowitzka (1972) found reduced macrophyte species diversity and biomass associated with shallow sewage discharge in New South Wales. Brown and red algae were totally absent from stations adjacent to the outfall. No animals were present at the outfall, and *Enteromorpha* spp. and *Chaetomorpha* sp. formed a dense algal mat throughout the intertidal. Recovery of these green algae in 1-m^2 sterilized areas of substrate at the outfall occurred within 2 months, while more complex algal assemblages at stations away from the outfall recovered within 12 months.

Munda (1974) studied the effects of sewage discharge on littoral algae in a landlocked fjord in western Norway (Bergen) and on the coast of the northern Adriatic at Rovinj and reported large changes in benthic algal associations. At the coastal site,

fucoids were eliminated from polluted shores (i.e., *Pelvetia canaliculata, Fucus spiralis, Fucus serratus, Ascophyllum nodosum, Fucus vesiculosus*) and replaced by *Enteromorpha* spp. associations. Immediately adjacent to the outfall, algal biomass was very much reduced and represented by *Blindingia minima* and blue-greens. Similarly, with increased sewage input to the fjord, the *Fucus vesiculosus* association was replaced by *Ascophyllum nodosum* or *Chondrus crispus*. An *Enteromorpha intestinalis–E. compressa* association dominated moderately polluted shores, while only a *Blindingia minima*–blue-green association was present at heavily polluted sites adjacent to the discharge.

Thom (1983) found that cover of *Fucus distichus* var. *edentatus* in Puget Sound decreased with increasing sewage pollution as well as with increasing wave exposure and depth. Bellan-Santini (1968) reported the disappearance of *Cystoseira stricta* in the presence of sewage in Marseille, France. Dawson's 1959 and 1965 surveys in southern California indicated that sewage had greatly altered intertidal communities, particularly at Whites Point. Recovery has followed changes in treatment and outfall location (Thom and Widdowson 1978; Harris 1983). Both the intertidal flora and fauna adjacent to a Carmel Bay, California, discharge were less diverse than at a control site (Abbott 1973). Only 50% of the algal species typical of the area were represented at the discharge site, while 85% were present at the control station.

It is generally recognized that ecological impacts of organic pollution such as pulp mill wastes on soft-bottom benthic communities is attributable to the long-term sedimentation and accumulation of organic matter and associated materials. While accumulated organic wastes have also been reported to impact hard-bottom subtidal communities (e.g., Christie and Green 1982), there is little information on effects of organic wastes on rocky intertidal habitats. This may be because these wastes do not accumulate on rocky shores.

Pearson (1980) noted that the effects of pulp mill effluent are largely mediated by: (1) deposition of suspended solids, (2) toxicity of constituents, (3) biochemical oxygen demand (BOD) of dissolved organics, and (4) effluent turbidity. Although changes in these parameters are more likely to affect soft-bottom subtidal communities, effects have been documented in rocky intertidal habitats. For example, Hellenbrand (1979) found some evidence for reduced productivity of *Fucus vesiculosus* exposed in the laboratory to treated Kraft mill effluent. Respiration was also reduced in *Chondrus crispus* and *Ascophyllum nodosum*, but no changes in photosynthesis were detected. Results of transplant experiments in the field indicated that algae maintained in close proximity to the outfall (600–2,100 m) showed increased rates of photosynthesis.

Cross and Ellis (1981) studied changes in the distribution and abundance of oligochaetes, *Fucus* epifauna, and rocky intertidal assemblages in a British Columbian "fjord" resulting from reductions in discharge of sulfite pulp mill wastes. Their data suggest that tolerance of littoral algae to pulp mill effluent varied with species and distance from the discharge. The order of tolerance of algal species was *Enteromorpha* > *Fucus* > *Ulva*.

D. Recreational Use

The ecological effects of recreational use of rocky intertidal shores represent impacts that differ greatly from those normally associated with pollution. We have little understanding of the biological responses to such disturbances as trampling (Liddle 1975). Trampling, "souvenir" collection, handling, bait collection, etc., also vary in time and space. Consequently, recreational impacts on rocky shores are not easily studied and data are difficult to interpret. Most of the published information is based upon qualitative observations made at high public use sites and inferences made from ecological surveys (e.g., Dawson 1965). Documentation relating recreational use to specific impacts is still very tenuous. Beauchamp and Gowing (1982) and Ghazanshahi et al. (1983) summarize the limited information on this subject.

Beauchamp and Gowing (1982) studied three rocky intertidal sites that varied in degree of public accessibility. Based upon destructive quadrat sampling and counts of people, species richness and density decreased with increased accessibility. This trend was more pronounced in the mussel bed assemblage than in other hard-substrate assemblages. Presence of *Pelvetiopsis limitata* and the bivalve *Lasaea* sp. varied directly with accessibility, while no differences in densities of mussels or barnacles, or in algal diversity were detected. Seasonal differences in invertebrate and algal densities were evident at all sites.

In a study of visitor impact on Anacapa Island, California, Littler (1978) surmised that algae with a high surface-to-volume ratio (e.g., filamentous and sheet forms) were indicative of stressful environments, i.e., increased human use.

In their review of the literature, Ghazanshahi et al. (1983) noted that Chan (1970) and Chan and Molina (1969) reported lower abundances of mussels, anemones, gastropods, and sea stars with greater human use. Similarly, Zedler (1976, 1978) found lower abundances of corralline algae, *Phragmatopoma californica, Collisella digitalis*, and large *Lottia gigantea* in areas of greater human use at Cabrillo National Monument, Pt. Loma, California. In their own study of 13 littoral sites around the Palos Verdes Peninsula, Ghazanshahi et al. (1983) listed species likely to be affected by public use (Table 7). Although sampling error, spatial and temporal heterogeneity, and other differences between sites contributed to substantial variation in the data, changes in abundances could be related to public use for some species, including *Mytilus californianus, L. gigantea, Pisaster ochraceus, Collisella digitalis, Balanus glandula*, and *Phragmatopoma californica*. No differences between sites were evident based upon total species numbers or diversity, even though changes in abundance were detectable. Abundant algae were more likely to be damaged by trampling than less abundant algae. Reduction in some of the algae was correlated with an increase in sessile invertebrates. Mobile invertebrates were less affected by trampling than sessile species. The authors concluded that recreational use can alter rocky intertidal ecosystems, and some types of recreational uses may have long-lasting effects (e.g., collection of long-lived limpets might alter grazing patterns for several years).

VI. Conclusions

The studies we have reviewed indicate that there are complex spatial and temporal patterns on rocky shores in central and northern California. At the large spatial scale of latitude, gradual and, in a few cases (e.g., Point Conception), fairly abrupt changes occur in intertidal species composition. Some of these changes

undoubtedly have secondary effects on associated species, but few of these effects have been examined (Sections II.A.1 and III.B.1). There is evidence that recruitment of some invertebrates may be more sporadic north of Point Conception (Section III.B.1.b), perhaps leading to more variable succession on more northerly shores. Studies needed to answer this question remain to be done.

Temperate rocky shores are renowned for their spatial variability between tide marks. There have been numerous descriptions of this zonation (Section I), and experimental studies have found a variety of causes (Sections II.A.2 and III.A.2). Spatial variability or patchiness within particular intertidal zones or assemblages also has been long recognized, but quantitative descriptions of these patterns are few, and experimental investigations of their causes are just beginning (Sections II.A.3 and III.A.4).

With the exceptions of seasonal changes in the high intertidal and splash zones, and changes associated with occasional severe storms and toxic chemical spills, temporal variability in this community is not as obvious or well documented as spatial variability. As discussed in Sections II.B and III.B, however, and emphasized by Connell and Sousa (1983), this apparent temporal stability may be an illusion resulting from lack of information on the demography of those species that are the visual dominants of intertidal assemblages.

It is apparent that numerous factors are responsible for spatial and temporal patterns on any particular rocky shore, with disturbances caused by wave action, grazing, and predation of special significance. Succession following such disturbances is a complex phenomenon that changes with the degree of disturbance, the life history characteristics of the organisms disturbed, dispersal, recruitment, and a variety of possible interactions among species. The importance of dispersal and recruitment to recovery from disturbance still remains largely unknown in this and other geographic regions; studies of these processes are essential if succession is to be better understood.

Discrete disturbances resulting from oil spills and other pollution events are often most extensive in the high intertidal and commonly result in a particular recovery sequence of ephemeral algae followed by perennial species (Section V). This sequence is perhaps a result of the removal of grazers that often selectively consume ephemeral species, and the removal of other organisms that would otherwise inhibit ephemeral algal recruitment. Ephemeral species persist when human disturbances become chronic. Studies of natural disturbance suggest that this may be because these species produce more propagules that disperse relatively far and readily colonize and grow rapidly on bare rock. They may also persist because biological disturbance is reduced in the continued absence of large grazers and predators, because recruits of sessile perennials are continuously killed, or as a result of some combination of these processes and life history characteristics.

Prior reviews of rocky intertidal communities in the northeastern Pacific have concluded that variation and instability are the norm rather than the exception (e.g., introductory quote; Castenholz 1967; Connell 1972), and this review substantiates that conclusion. In this context, it is refreshing to note that since the reviews by Castenholz and Connell, a major shift has occurred in intertidal research from descriptive–correlative studies and searches for single factors to explain pattern (e.g., tidal factors, all important predators or grazers, competition) to investigations that describe and examine a variety of processes over a range of temporal and spatial scales. We now know much more about the causes of variation. Additional research on community and demographic patterns, combined with descriptive work at more sites, should provide the larger context needed to evaluate the generalizations that emerge.

TABLE 7. ROCKY INTERTIDAL SPECIES LIKELY TO BE AFFECTED BY PUBLIC USE (TRAMPLING, OVERTURNING ROCKS, COLLECTIONS; FROM GHAZANSHAHI ET AL. 1983).

Algae	Invertebrates
CHOSEN FROM GENERAL SURVEY RESULTS	
Egregia menziesii	*Tegula funebralis*
Corallina vancouveriensis	*Collisella conus*
Rhodoglossum affine	*Notoacmaea fenestrata*
Gigartina spinosa	*Nuttallina fluxa*
Mastocarpus papillatus	*Chthamalus* sp.
Gigartina leptorhynchos	*Balanus glandula*
Gigartina canaliculata	*Serpulorbis squamigerus*
Gelidium pusillum	
Chondria californica	
Colpomenia perigrina	
Ulva sp.	
Enteromorpha sp.	
CHOSEN FROM LITERATURE REPORTS	
	Strongylocentrotus purpuratus
	Collisella scabra
	Collisella digitalis
	Anthopleura sp.
	Tetraclita squamosa
	Pollicipes polymerus
	Lottia gigantea
	Phragmatopoma californica
	Mytilus californianus
	Pisaster ochraceus

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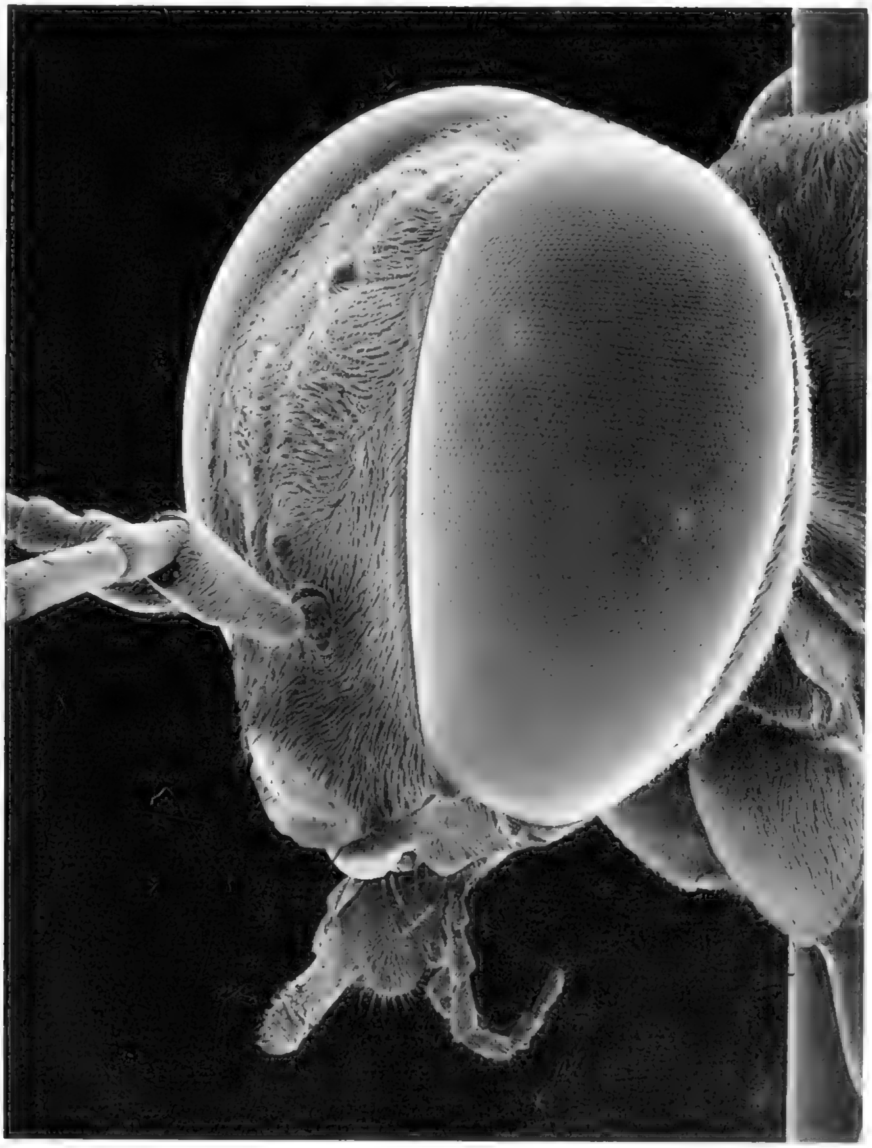
By Wojciech J. Pulawski



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Cover Illustration: Head of *Tachysphex ashmeadii*, a female. Photo by W. Pulawski and M. A. Tenorio.

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Contents

Abstract

North and Central American as well as Caribbean wasps of the genus *Tachysphex* are revised (totaling 83 species). Descriptions, illustrations, geographic records, distribution maps, and keys to the species identification are provided. The life histories are summarized and interpreted. A cladistic analysis is given for the *terminatus* species group. Twenty species are new: *angelicus* (western United States), *cocopa* (southwestern United States, western Mexico), *dominicanus* (Hispaniola), *hopi* (western United States), *huchiti* (western United States, Mexico), *maya* (Mexico, Costa Rica), *miwok* (California and adjacent areas), *oasicola* (western United States), *opata* (western United States, Mexico), *orestes* (western North America), *paiute* (California, Baja California), *pinal* (western United States, Mexico), *quisqueyus* (Hispaniola), *scopaeus* (Texas), *sulcatus* (California, Baja California), *tahoe* (western United States, Baja California), *tipai* (western United States, Mexico), *toltec* (Mexico), *tsil* (western United States, Mexico), and *utina* (southeastern United States). *Tachysphex aequalis* W. Fox and *robustior* Williams, previously sunk to subspecific status, are recognized as full species. The following are newly established synonyms: *pompiliformis* (Panzer, 1805) =*parvulus* (Cresson, 1865), *quebecensis* (Provancher, 1882), *decorus* W. Fox, 1894, *tenuipunctus* W. Fox, 1894, *erythraeus* Mickel, 1916, and *angularis* Mickel, 1916; *psammobius* (Kohl, 1880) =*sculptilis* W. Fox, 1894.

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Introduction

General.—This paper is a continuation of my worldwide studies of the genus *Tachysphex*. I previously revised the Palearctic species (Pulawski 1971), the Neotropical species (Pulawski 1974*a*), and the Australian species (Pulawski, 1977*a*). The North American species have not been systematically studied since W. Fox (1894*a*) and Williams (1914). As a result, many species (some of them common and widely distributed) were unnamed; numerous phena of unclear status needed to be recognized either as full species or individual variants; identification of most species was extremely difficult due to lack of reliable keys; and, in some cases, two or more names were simultaneously used for the same species. At present, 83 species have been defined, of which 20 are new. I was not able to define several phena that may represent a dozen or so species.

Since this study extended over a long period, preliminary diagnoses of 19 new species were published earlier (Pulawski 1982). Also, as a part of this project, I established several new synonyms (a few of them erroneously) in Krombein (1979). As a historical curiosity, the project started in Washington, D.C., while I was on a postdoctoral fellowship at the Smithsonian Institution (1974–75), was carried over in the Natural History Museum, Wroclaw University, Poland (1975–80), and completed at the California Academy of Sciences, San Francisco (1981–86).

Although this study is regional in scope, morphological characters and life histories are treated on a worldwide basis insofar as possible.

Technical Terms and Symbols.—I follow Bohart and Menke (1976) in their usage of morphological terms, but a few terms and symbols need clarification or are redefined here for convenience. They are:

Axilla: topographically the anterolateral part of the scutellum (morphologically a part of the scutum).

Clypeus (Fig. 1): has a middle section and two lateral sections. The middle section usually has a densely punctate, setose basomedian area, a sparsely punctate, shining bevel, and a marginal lip. The prominent part of the middle section is often referred to as the lobe. The free margin of the lobe can be straight, concave, sinuate, arcuate, or biarcuate; the lip can have a mesal emargination, and/or one or two lateral incisions. The clypeal length is measured along the body's longitudinal axis.

Disk: the central part of a sclerite, e.g., scutal disk, tergal disk.

Frons: the area between the frontoclypeal suture and hindocellus.

Graduli: a pair of oblique furrows on sternum II and the following ones.

Hindcoxa carinate: with a carina on the inner dorsal margin.

Humeral plate of forewing: a sclerotized plate located basad to the costal and subcostal veins and partly covered by the tegula.

Mandibular acetabulum: mandibular articulation adjacent to the clypeus.

Mandibular condylus: mandibular articulation opposite the acetabulum.

Median plate of forewing: a small, elongate plate between the anal vein and the tegula.

Mesothoracic venter: the part of thorax between forecoxa and midcoxa.

Metapleural flange: a horizontal, lamellar expansion of the metapleural dorsal margin.

Micropunctures: punctures of very small size, significantly smaller than those on scutum.

MOD: midocellar diameter.

Postspiracular carina: a vertical or subvertical carina on the mesopleuron behind the pronotal lobe.

Scutum: abbreviation for mesoscutum.

Setae appressed, erect, inclined: forming an angle of approximately 0°, 90°, or an intermediate angle with the body surface, respectively.

Subcontiguous: nearly touching each other.

Tergum, sternum: abbreviations for gastral tergum, gastral sternum.

Vertex length (Fig. 2): the distance between a hindocellus and an imaginary line connecting the eye hindcorners (i.e., the point where the inner and the posterior portions of the orbit meet).

Vertex width (Fig. 2): the shortest interocular distance.

! followed by the word holotype, lectotype, or neotype in bibliographic citations: indicates that I have examined the specimen.

— after the state, province, or county name in Records sections: the county or specific locality unknown.

Male Genitalia.—Generally in *Tachysphex*, male genitalia and especially the shape of the volsella provide important recognition features. This is not the case among the North American species. Only a few have a distinctive volsella or penis valve (illustrations have been provided in these instances). In most species, including all of the *pompiliformis* group, the gen-

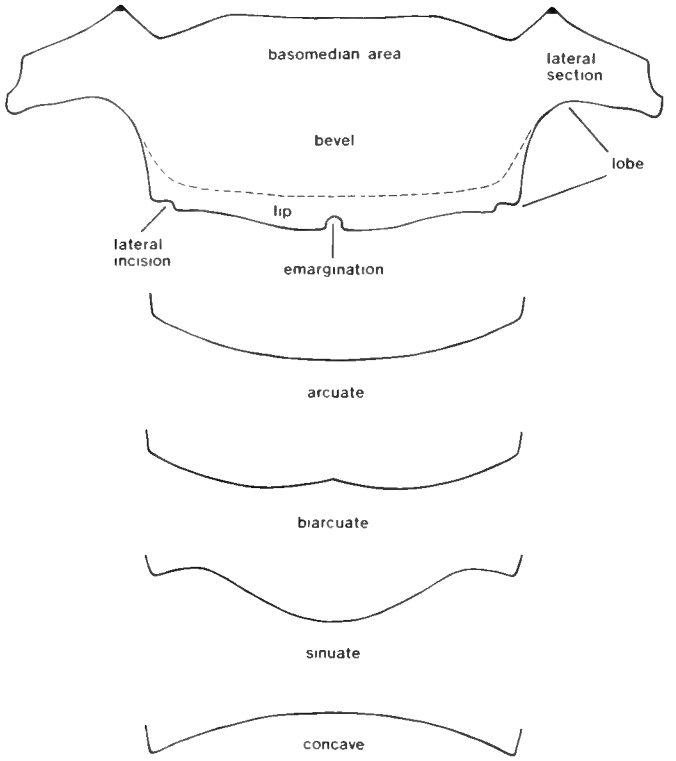

FIGURE 1. Clypeus of *Tachysphex*

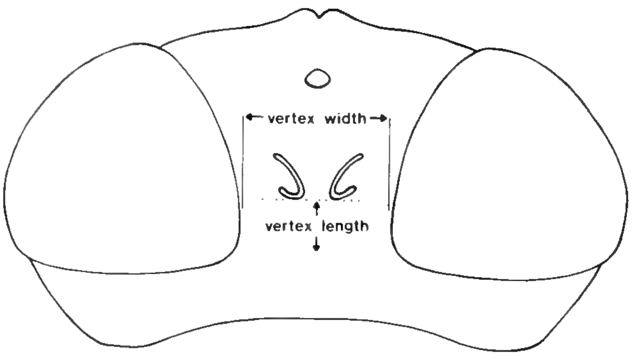

FIGURE 2. Vertex of *Tachysphex*.

ital organs are similar and individually variable, so that they are useless for diagnostic purposes. A striking example of individual variation is provided by *Tachysphex acanthophorus* in which the dorsal process of the volsella may be higher than wide or markedly lower than wide, with all possible intermediates.

LOCALITY RECORDS.—All place names listed under Records have been checked against available maps or gazetteers, and names not found there have been excluded. Also excluded are conflicting data (such as labels that place localities in the wrong county). After verification, the locality lists were used to produce the distribution maps. If a species has been found in more than three localities within a county, usually only the county name is listed. The same rule has been applied, in some cases, to the Mexican states of Baja California Norte and Baja California Sur.

Altitudes and distances are given as they appear on the original labels—mostly in feet and miles, because the metric system is not widely used in the United States, and distances and altitudes on most maps and atlases are given in English units.

SOURCES OF MATERIAL.—More than 40,100 specimens have been examined. I collected many in the United States, Mexico, and the Caribbean Islands during seven seasons (frequently helped by my wife Veronica E. Ahrens), but most were made available for study by institutions and individuals. In the Species Descriptions section, sources of material are indicated for all new species as well as for previously described rare species, but are omitted for common species. The following is a list of sources and persons who arranged the loans (the abbreviations preceding the names are used in the text to designate these collections):

AMNH American Museum of Natural History, New York, New York (M. S. Favreau)

ANSP. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (D. C. F. Rentz)

ASU: Arizona State University, Department of Zoology, Tempe, Arizona (F. F. Hasbrouck).

BISH Bernice P. Bishop, Museum, Honolulu, Hawaii (F. J. Radovsky).

BMNH British Museum (Natural History), London, England (C. R. Vardy).

BU Boston University, Department of Biology, Boston, Massachusetts (S. Duncan)

CAS California Academy of Sciences, San Francisco, California (P. H. Arnaud, Jr., W. J. Pulawski, T. J. Zavortink).

CIS California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California (J. A. Chemsak, H. V. Daly)

CNC Canadian National Collections of Insects, Arachnids, and Nematodes, Biosystematics Research Institute, Ottawa, Ontario (J. R. Barron).

CPDA Commonwealth of Pennsylvania Department of Agriculture, Bureau of Plant Industry, Harrisburg, Pennsylvania (E. E. Simons).

CSDA California Department of Food and Agriculture, Sacramento, California (M. S. Washauer)

CSU Colorado State University, Department of Zoology and Entomology, Fort Collins, Colorado (H. E. Evans)

CU Cornell University, Department of Entomology and Limnology, Ithaca, New York (L. L. Pechuman)

FCDA: County of Fresno Department of Agriculture, Fresno, California (N. J. Smith)

FMNH Field Museum of Natural History, Chicago, Illinois (R. L. Wenzel).

FSCA Florida State Collection of Arthropods, Gainesville, Florida (E. E. Grissell, L. A. Stange, J. Wiley)

HKT Henry K. Townes, American Entomological Institute, Ann Arbor, Michigan (now Gainesville, Florida)

HSU Humboldt State University, Department of Biological Sciences, Arcata, California (D. M. Gordon)

IJ Institute of Jamaica, Kingston, Jamaica (T. H. Farr).

INHS Illinois State Natural History Survey, Urbana, Illinois (W. E. LaBerge).

ISU Iowa State University, Department of Entomology, Ames, Iowa (the late J. L. Laffoon)

KSU Kansas State University, Department of Entomology, Manhattan, Kansas (H. D. Blocker)

KU University of Kansas, Snow Entomological Museum, Lawrence, Kansas (R. W. Brooks, G. W. Byers)

KVK Karl V. Krombein, Arlington, Virginia (pers. coll.), now in USNM.

KWC Kenneth W. Cooper, Riverside, California (pers. coll.)

LACM Natural History Museum of Los Angeles County, Los Angeles, California (R. R. Snelling)

LBSC California State College at Long Beach, California (E. L. Sleeper).

LEM MacDonald College of McGill University, Lyman Entomological Museum, Ste. Anne de la Bellevue, Quebec (A. T. Finnamore)

MCZ Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (J. F. Lawrence, J. C. Scott, M. K. Thayer)

MOB Mark F. O'Brien, Ann Arbor, Michigan (pers. coll.)

MPM Milwaukee Public Museum, Milwaukee, Wisconsin (J. K. Lawton)

MSU Montana State University, Department of Zoology and Entomology, Bozeman, Montana (N. L. Anderson)

NCSU: North Carolina State University, Department of Entomology, Raleigh, North Carolina (C. S. Parron, D. A. Young).
NHMV: Naturhistorisches Museum, Vienna, Austria (M. Fischer).
NSDA: Nevada State Department of Agriculture, Reno, Nevada (R. C. Bechtel).
NYSU: New York State University, College of Environmental Science and Forestry, Department of Environmental and Forest Biology, Syracuse, New York (F. E. Kurczewski).
OSDA: State of Oregon Department of Agriculture, Salem, Oregon (R. L. Westcott).
OSU: Oregon State University, Department of Entomology, Corvallis, Oregon (G. R. Ferguson, P. W. Oman).
RBP: Robert B. Parks, % San Diego Natural History Museum, San Diego, California (pers. coll.).
SDNH: San Diego Natural History Museum, San Diego, California (D. K. Faulkner).
TAI: Texas A&I University, Kingsville, Texas (J. E. Gillaspy).
TAM: Texas A&M University, Department of Entomology, College Station, Texas (H. R. Burke)
TLG: Terry L. Griswold, % Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah (pers. coll.).
UAE: University of Alberta, Department of Zoology, Edmonton, Alberta (A. L. Steiner).
UAF: University of Arkansas, Department of Entomology, Fayetteville, Arkansas (E. P. Rouse).
UAT: University of Arizona, Department of Entomology, Tucson, Arizona (C. A. Olson, F. G. Werner)
UCD: University of California, Department of Entomology, Bohart Museum, Davis, California (R. M. Bohart, R. O. Schuster).
UCR: University of California, Department of Biological Control, Riverside, California (S. I. Frommer).
UFG: University of Florida, Department of Entomology and Nematology, Gainesville, Florida (B. Saffer).
UGA: University of Georgia, Department of Entomology, Athens, Georgia (R. W. Matthews, C. L. Smith)
UIM: University of Idaho, Department of Entomology, Moscow, Idaho (W. F. Barr, J. B. Johnson)
UMA: University of Massachusetts, Department of Entomology and Plant Pathology, Amherst, Massachusetts (M. E. Smith).
UMMZ: University of Michigan, Museum of Zoology, Ann Arbor, Michigan (T. E. Moore, M. F. O'Brien)
UMSP: University of Minnesota, Department of Entomology and Zoology, St. Paul, Minnesota (P. J. Clausen)
UNL: University of Nebraska State Museum, Lincoln, Nebraska (B. C. Ratcliffe).
USNM: United States National Museum of Natural History (Smithsonian Institution), Washington, D.C. (K. V. Krombein, A. S. Menke)
USU: Utah State University, Department of Zoology, Logan, Utah (G. E. Bohart, F. D. Parker).
UW: University of Wisconsin, Department of Entomology, Madison, Wisconsin (L. J. Bayer)
WJP: Wojciech J. Pulawski, % California Academy of Sciences, San Francisco, California (pers. coll.).
WSU: Washington State University, Department of Entomology, Pullman, Washington (the late M. T. James, R. S. Zack)
ZMB: Zoologisches Museum der Humboldt Universitat, Berlin, German Democratic Republic (the late E. Königsmann).

Collectors' Names.—Collectors of specimens in type series of new species are abbreviated as follows (names mentioned once or a few times are not abbreviated):

ASM: Arnold S. Menke
DKF: David K. Faulkner
DSH: Donald S. Horning
EEG: E. Eric Grissell
EGL: E(arl) Gorton Linsley
EIS: Evert I. Schlinger
FDP: Frank D. Parker
FXW: Francis X. Williams
GEB: George E. Bohart
HEE: Howard E. Evans
HKC: Helen K. Court
JAP: Jerry A. Powell
JEG: James E. Gillaspy
JWB: John W. Brown
JWMS: John W. MacSwain
KWC: Kenneth W. Cooper
LAS: Lionel A. Stange
MEI: Michael E. Irwin
MSW: Marius S. Wasbauer
NJS: Norman J. Smith
PDH: Paul D. Hurd
PHA: Paul H. Arnaud, Jr.
PMM: Paul M. Marsh
RCB: Robert C. Bechtel
REC: Rollin E. Coville
TLG: Terry L. Griswold
TRH: Thomas R. Haig
WFB: William F. Barr
WJP: Wojciech J. Pulawski
WWM: Woodrow W. Middlekauff

Acknowledgments.—The project was supported by a year-long postdoctoral fellowship from the Smithsonian Institution in 1974–75, by grants from the Polish Academy of Sciences in 1976–80, five grants from the California Academy of Sciences In-House Research Fund in 1982–86, and the G. Lindsay Fund for Field Research. I sincerely thank all persons who sent me material for study and also other persons for their support and active help. Only some of them are listed here. Arnold S. Menke arranged most loans, significantly influenced the organization of this paper, read all descriptions (some of them many times), offered a cross-country collecting trip in 1975, and helped morally and materially in many other ways. Karl V. Krombein, equally friendly and helpful, took me on a collecting trip to Florida in April 1975 and commented on the manuscript. I owe thanks to Richard M. Bohart for two collecting trips to Borrego Valley, California (springs of 1975 and 1981), fruitful criticism, and friendly support. Baldomero Villegas took me to the Mt. Shasta area, California, in June 1981, and Dennis E. Breedlove to Baja California in March 1984 and to continental Mexico in September 1984. Robert E. Woodruff gave valuable assistance during my trip to the Dominican Republic, and Thomas H. Farr and Bryan E. Freeman helped organize fieldwork in Jamaica. Grażyna Zdunek typed countless early drafts of the text in Wrocław, Poland in 1975–80, drew the first version of distribution maps, and helped in many other ways. L. Gail Freihofer typed the manuscript on an NBI word processor in 1982. Mary Ann Tenorio produced the final version of the distribution maps and the scanning electron micrographs in 1983–86, and patiently helped with grammar, style, and editing. Thomas Duncan and David L. Wagner helped with cladistic analysis. Many persons helped in locating obscure locality names. My wife, Veronica E. Ahrens, willingly endured the hardships of many collecting trips and significantly contributed to the number of specimens and species collected. The nearly final version of the manuscript was reviewed, at my request, by Paul H. Arnaud, Jr., Helen K. Court, Frank E. Kurczewski, and Arnold S. Menke. Richard M. Bohart volunteered to review the introduction and the key, and Vincent F. Lee checked the manuscript for spelling and consistency. All suggested innumerable improvements.

Genus *Tachysphex* Kohl

Tachysphex Kohl, 1883:166. Type species: *Tachysphex filicornis* Kohl, 1883 (=*Tachytes fugax* Radoszkowski, 1877), designated by Bingham 1897:192.
Atelosphex Arnold, 1923:177. Type species: *Atelosphex miscophoides* Arnold, 1923, by original designation and monotypy. Synonymized with *Tachysphex* by Pulawski 1971:9.

Morphology.—*Tachysphex* does not have a single autapotypic character state (=apotypic character state not found elsewhere), and thus it is not holophyletic according to the cladistic school. However, it certainly is not an artificial assemblage of unrelated species: any two species of *Tachysphex* are more similar to each other than to representatives of any other genus currently recognized, and it is more likely that their similarity is due to common origin rather than to convergence.

The modern morphological characterization of *Tachysphex* given by Bohart and Menke (1976) was refined by me (Pulawski 1979). All pertinent structural characters of the genus currently known are also reviewed below and compared with homologous features in *Holotachysphex* de Beaumont, *Parapiagetia* Kohl, and *Prosopigastra* A. Costa, the closest relatives of *Tachysphex*. These four genera form a single evolutionary branch within Larrini (Bohart and Menke 1976).

1) Frons with oblong, glabrous tubercle above each antennal socket; tubercles convergent above. These are also present in *Holotachysphex* and *Parapiagetia*, but absent in *Prosopigastra*.

2) Propodeal enclosure setose except glabrous in *sinaiticus* (Sinai Peninsula), many *tenuis* (Australia), and largely glabrous in many *walkeri* Turner. The enclosure is setose in *Holotachysphex*, setose or posteriorly glabrous in *Parapiagetia*, and glabrous in *Prosopigastra*.

3) Tergum I without short, oblique carina extending from each anterolateral corner. This carina is also absent in *Holotachysphex* and *Parapiagetia*, but present in *Prosopigastra*.

4) Tergum II not carinate laterally (most species). Menke (*in* Bohart and Menke 1976) stated that a sharp, lateral carina is only present on tergum I in *Tachysphex* and *Parapiagetia*, but that I and II are carinate laterally in *Holotachysphex* and *Prosopigastra*. Actually, a weak carina is also present on tergum II in some large Australian *Tachysphex*, especially females, e.g., *hypoleius*, *persistans*, *pugnator*, and *stimulator*. Also, the lateral carina of tergum II is rudimentary or absent in *Prosopigastra creon* and *nubigera* (Pulawski 1979).

5) The angle between the lateral margin of female tergum VI and the lateral margin of the pygidial plate, in side view, is about 30–40° in the apical third (tergum not flattened). This angle is similar in *Holotachysphex* and *Parapiagetia*, but much narrower (10–20°) in *Prosopigastra* (tergum flattened).

6) Female with pygidial plate except evanescent in the Old World *erythropus*, the South American *mendozanus*, and absent in the Australian *nefarius*. Present also in *Parapiagetia* and *Prosopigastra*, but absent in *Holotachysphex*.

7) Pygidial plate of female simple, except for a transverse, preapical row of punctures in the Old World species *costae* and *erythropus* and in the Australian *multifasciatus*. The pygidial plate is also simple in *Parapiagetia*, but in *Prosopigastra* it has a preapical, arcuate row of setigerous punctures that extends anterad along the marginal carina.

8) Sting circular in cross section. Similar in *Holotachysphex*, but flattened dorsoventrally in *Parapiagetia* and *Prosopigastra*.

9) Male tergum VII not depressed apically. Similar in *Holotachysphex* and *Parapiagetia*, but a translucent, impunctate apical depression is present in *Prosopigastra* (depression delimited by a row of punctures, which are evanescent in *P. ahrensiana* and *menelaus*).

10) Marginal cell of forewing not shortened, narrowly truncate apically: foremargin 2.7–4.2 × maximum width (inner dimensions), and the distance between posteroapical corner and the wing foremargin is 0.2–0.6 × maximum width. Marginal cell similar in *Holotachysphex* (same ratios: 2.7–3.5 and 0.5) and *Parapiagetia* except shorter in the *odontostoma* group (ratios: 1.1–3.6 and 0.3–0.9), shortened and more truncate apically in *Prosopigastra* (ratios: 1.6–2.3 and 0.6–0.9).

11) Forecoxal apex without apical process, except with an apical process in *Tachysphex bohartorum* and *hopi*. Process absent in *Holotachysphex* and *Parapiagetia*. A similar but nonhomologous process present in *Prosopigastra*.

12) Hindtarsomere II 0.5–0.7 × length of hindtarsomere I, 0.6–0.7 in *Holotachysphex* and most *Parapiagetia* (about 0.5 in *Parapiagetia mongolica*, but 0.3–0.4 in *Prosopigastra*).

13) No additional sclerites between the metasternal apex and propodeum. Similar in *Holotachysphex* and *Prosopigastra*, but a pair of sclerites ("propodeal sternum" of Menke *in* Bohart and Menke 1976) present in *Parapiagetia*.

14) Male forefemur notched in most species (entire in *Tachysphex antillarum*, *dominicanus*, *sericeus flavofimbriatus*, *maculipennis*, *quisqueyus*, *tenuis*, *vitiensis*, some *psilocerus*, and in the *geniculatus* species group). Forefemur notched in *Holotachysphex*, but entire in *Parapiagetia* and *Prosopigastra*.

15) Male sterna without velvety patches. Such patches are present in *Holotachysphex*, but absent in *Parapiagetia* and *Prosopigastra*.

16) Female foretarsus with a rake which consists of long, flexible setae. The rake is also present in *Parapiagetia* and *Prosopigastra*, but absent in *Holotachysphex*.

Life History.—In this section I review 27 behavioral components and discuss behavioral differences among species. Nearctic species are given special emphasis. Species from other zoogeographic regions are mentioned only when their behavior is known to differ. Detailed information on 25 Nearctic species is provided in this paper under Descriptions of the Species (where bibliographic references can be found). The life histories of 17 Palearctic species were summarized by Pulawski (1971). Later, I (Pulawski 1974*b*) observed the nesting habits of two additional species. Habits of Australian species have been elucidated mainly by Evans et al. (1976), but also by a few previous authors. Data for these seven species were summarized by Pulawski (1977*a*). Observations of three Neotropical species were summarized by Pulawski (1974*a*). Arnold (1945) briefly mentioned the prey of four Madagascan species, and Gess (1981) briefly described nesting habitats of seven South African species.

For each biological component, a list is given of Nearctic species in which this component has been documented.

1) *Generations*. Among North American species, there is one generation per year in *laevifrons*, *pompiliformis*, and *pechumani* (in which an obligate diapause is thus probable), two in *crassiformis*, two or more in *krombeini*, and two in *terminatus* (possibly up to five in southern Texas). The number of generations per year was not studied in non-Nearctic species.

2) *Food of adults*. Flower nectar is a common food, but honeydew is also important (*acutus*, *aequalis*, *alpestris*, *angelicus*, *antennatus*, *apicalis*, *apricus*, *ashmeadii*, *belfragei*, *coquilletti*, *hopi*, *krombeiniellus*, *mundus*, *musciventris*, *opata*, *pauxillus*, *pompiliformis*, *punctifrons*, *similis*, *tahoe*, *tarsatus*, *terminatus*, *texanus*, *tipai*, *verticalis*, *yolo*).

3) *Relation of provisioning to nest digging*. Nest excavation by the female precedes hunting and oviposition (*aethiops*, *ashmeadii*, *clarconis*, *mundus*, *pechumani*, *semirufus*, *terminatus*).

4) *Nest site selection*. Nests are established in the soil (*aethiops*, *alpestris*, *apicalis*, *ashmeadii*, *belfragei*, *clarconis*, *coquilletti*, *crassiformis*, *inconspicuus*, *krombeini*, *laevifrons*, *mundus*, *pauxillus*, *pechumani*, *pompiliformis*, *psammobius*, *punctifrons*, *semirufus*, *similis*, *terminatus*, *texanus*).

5) *Nest placement*. Most species nidify on horizontal or inclined substrates but *apicalis* and also the Old World species

fugax and *costae* dig their nests exclusively in sloping banks of cliffs. Also, *terminatus* occasionally nidifies on sloping surfaces. Kurczewski and Snyder (1968) pointed out that nest placement in sloping banks implies: (1) the soil excavated from the nest rolls down and cannot be reused for nest closure (thus the nest is permanently open during the provisioning period), (2) soil from the sides and top of the burrow is used for the final closure, and (3) the female arriving at the nest with prey enters the burrow without pausing at the nest entrance.

6) *Use of preexisting nests.* Most species dig their own nests, but *mundus* and also two Old World species (*costae* and *plicosus*) use galleries of other aculeates. Burrows of other wasps are occasionally adapted for nests (*aethiops*). Females of *Prosopigastra* also establish their nests in burrows of other aculeates. Kurczewski (1979) demonstrated that *mundus* digs its nest in the wall of a preexisting gallery, a possibility that was not considered by authors observing the habits of *costae, plicosus,* and *Prosopigastra. Prosopigastra* and also *Tachysphex costae, mundus,* and *plicosus* have a long, dense foretarsal rake, contrasting with the shorter, sparser rake of the species that start their nest from the hard surface of the soil. This suggests a correlation between nesting behavior and structure of the foretarsal rake.

7) *Digging.* When starting a nest, the female first scratches the soil with her mandibles. She subsequently uses her forelegs in unison to rake away soil. The antennae are stretched out, and their apices touch the soil. From time to time she stops digging, walks away from the nest, and then walks towards the orifice while throwing the excavated soil with her hindlegs (*ashmeadii, pechumani, similis*). The material evacuated from the nest streams behind the wasp.

8) *Angle of nest burrow.* The burrow is never vertical. It forms an oblique angle with the surface in *aethiops, ashmeadii, krombeini, pechumani, pompiliformis, psammobius, punctifrons, semirufus, similis, tarsatus, terminatus,* and *texanus.* It is almost horizontal in *apicalis,* which nidifies on sloping banks or cliffs, and in *mundus,* which starts its own nests from preexisting burrows of other aculeates. In these species, material flows backwards in a constant stream during nest excavation. This would be impossible in vertical galleries. In fact, species that establish vertical nests either push the material backwards using abdomen (*Cerceris*) or hindlegs (*Astata*), or remove it with their mandibles (*Ammophila*).

9) *Tumulus.* In most species, the material excavated from the nest accumulates at the entrance as a tumulus (*aethiops, ashmeadii, krombeini, pauxillus, psammobius, punctifrons, pechumani, semirufus, tarsatus*). The tumulus is leveled in three species (all Nearctic): *clarconis, similis,* and *terminatus,* a habit apparently associated with temporary closure of the nest. The tumulus is slightly flattened in *pechumani* in which there is a rudimentary temporary closure of the nest.

10) *Orientation flight.* After completion of the nest, the female performs an orientation flight before leaving the nest area (*ashmeadii, clarconis, coquilletti, mundus, psammobius, tarsatus*). The female of *pechumani* performs orientation walks around the nest.

11) *Temporary closure.* During the provisioning period, the nest is permanently open in some species (*apicalis, ashmeadii, belfragei, crassiformis, krombeini, mundus, pauxillus, pompiliformis, psammobius, punctifrons, semirufus, tarsatus, texanus*). In others, it is closed except when the female is inside (*alpestris, clarconis, terminatus,* and also *pechumani,* in which the closure may be incomplete). Gess (1981) found that the nest entrances of two South African *Bembecinus* that nidify in sand (*braunsii* and *haemorrhoidalis*) are permanently open during the wasp's working day, but the nests of two other species that nidify in clay (*cinguliger* and *oxydorcus*) are closed except when the female is inside. It is not known whether this correlation is also valid for *Tachysphex.*

12) *Nest structure.* The nest consists of a gallery and one to six larval cells (*aethiops, alpestris, apicalis, ashmeadii, coquilletti, crassiformis, krombeini, pauxillus, pechumani, pompiliformis, psammobius, punctifrons, semirufus, similis, tarsatus, terminatus, texanus*). It is unicellular in several species.

13) *Prey.* Various orthopteroid insects are used as prey, namely: (1) Acrididae (*brevipennis, panzeri,* and *undatus* groups, most members of the *pompiliformis* group), (2) Tettigoniidae (some species of the *brullii* group; three species of the *pompiliformis* group: *semirufus, tipai,* and the Palearctic *fulvitarsis*; partly also *plicosus* of the *plicosus* group), (3) Grylllidae of the genus *Oecanthus* (main prey in the *plicosus* group, partly also *mundus* of the *brullii* group), (4) Blattidae (some species of the *brullii* group), and (5) Mantidae (*albocinctus, erythropus, julliani,* and *schmiedeknechti* groups). Elliott and Kurczewski (1985) listed a phasmid as prey of *apricus,* a record based on a paratype female pinned with *Parabacillus hesperus.* This association may be erroneous. Prey is unknown for the *euxinus, geniculatus, isis, mendozanus,* and *nefarius* groups, but their relationships suggest that members of the *euxinus* and *geniculatus* groups are acridid hunters, while those of the *isis* group are mantid collectors. Insects of one family are usually stored as prey, but representatives of two families have been found in four species: in *plicosus* (see Pulawski 1974*b*) and *mundus* (see Kurczewski 1979), in which tree crickets of the genus *Oecanthus* (Oecanthidae) were mixed with tettigoniids, in *terminatus* (see Kurczewski 1966*a*), which usually collects acridids but occasionally preys on tettigoniids, and in a nest of *krombeini* (see Kurczewski 1971) that contained six acridid nymphs and one tettigoniid nymph. In the last two species, the prey represent two different orthopteran suborders. Arnold (1945) mentioned that *micromegas,* a Madagascan species, collected "immature crickets and grasshoppers," but he gave no details, and his statement needs confirmation. Collecting members of two families may be normal because of their similar appearance.

14) *Stinging posture.* The female of *Tachysphex pechumani* pounces on a grasshopper, grasps it with her claws, orients her body transversely, bends the tip of her abdomen toward the ventral side of the grasshopper, and inserts the sting (Kurczewski and Elliott 1978). The grasshopper can prevent the wasp from stinging (Steiner 1982) by raising the hindlegs and freezing, or by biting (a female of *tarsatus* was severely bitten by a larva of *Trimerotropis pallidipennis* during a stinging attempt and died the following day), or by regurgitating fluids (a female of *tarsatus,* her gastral tip covered with sticky substance and sand grains, was found dying, presumably as the result of an unsuccessful attempt at paralyzing prey).

15) *Number of stings.* Steiner (1962) first established (in *Liris niger*) that during paralyzing the sting is inserted into the ventral side of the prey's body mainly in small membranous areas that he called stinging sites. Their number and location correspond to the number and location of the prey's main nerve ganglia. In

Tachysphex pompiliformis and *tarsatus*, stinging sites on grasshopper prey are (Steiner 1981): posteroadmedially on the head (for the subesophageal ganglion), admedially at the level of the forelegs (for the prothoracic ganglion), admedially between the fore- and midlegs and adjacent to the previous site (for the mesothoracic ganglion), and laterally between mid- and hindlegs (for the metathoracic ganglion). The number of stings may be equal to the number of stinging sites (also confirmed by Steiner's direct laboratory observations), or may be less (incomplete sequence), or rarely the stings or the stinging sequence may be repeated ("stinging frenzy"). In the past, various European authors, Sibuya (1933) and also Kurczewski and Elliott (1978; in *pechumani*), reported that the prey is paralyzed with one to three stings.

16) *Stinging sequence.* The stinging sequence is hindlegs, forelegs, midlegs, and mouthparts in the grasshopper collectors *pompiliformis* (as "unidentified species") and *tarsatus* (see Steiner 1981). This sequence contrasts with habits of *Prionyx parkeri*, another grasshopper collector, which first paralyzes the mouthparts and then the forelegs, midlegs, and hindlegs (Steiner 1981). *Tachysphex costae*, which preys on mantids, first paralyzes the raptorial forelegs (summary in Pulawski 1971; also Steiner 1981: 329).

17) *Cephalic mastication.* Mastication of prey's head to obtain fluids has been reported for *ashmeadii* and also for two Old World species (*albocinctus* and *brullii*). Mastication of the prey "near the area of the sting puncture" by a female of *psammobius* was reported by Kurczewski (1987).

18) *Type of prey transportation.* When carrying the prey, the female holds it by the antennal base with her mandibles and moves headfirst in *ashmeadii, belfragei, clarconis, crassiformis, krombeini, mundus, pauxillus, pechumani, pompiliformis, semirufus, similis, tarsatus*, and *terminatus*. This is the Mandibular Type Two of Evans (1962).

19) *Prey position during transportation.* Most authors report that the prey is carried venter down, including in *mundus*, but Kurczewski (1971) reports that the prey is transported venter up in *krombeini*. *Tachysphex terminatus* carries the prey venter up according to Kurczewski (1966*a*) and venter down according to Strandtmann (1953). William's (1914) description suggests that prey of *ashmeadii* and *tarsatus* are kept venter up. Perhaps the prey is carried in the position in which it is paralyzed.

20) *Aerial and terrestrial prey transportation.* The prey is carried on the ground, or in a series of short flights, or in one continuous flight (*alpestris, ashmeadii, belfragei, clarconis, crassiformis, krombeini, mundus, pauxillus, pechumani, pompiliformis, psammobius, punctifrons, similis, tarsatus, terminatus, texanus*). In *pechumani*, the prey is flown if its weight does not exceed twice the female's weight; heavier prey (up to six times the female's weight) is transported on the ground.

21) *Entering nest with prey.* In most species, the female deposits the prey at the nest entrance, opens it (if the nest is temporarily closed), and then enters. She turns around inside, pokes her head out of the nest entrance, grabs the prey with her mandibles, and pulls it inside (*clarconis, krombeini, pechumani, pompiliformis, similis, terminatus*). Females of *ashmeadii* and *mundus* (that fly with prey) enter the nest directly, and so does the female of *punctifrons* (that walks with prey). Females of *crassiformis, psammobius, tarsatus*, and *texanus* either drop the prey or enter the nest directly. Females of two Old World species, *mediterraneus* and *albocinctus*, open the nest without dropping the prey (this method apparently protects the nest and the prey better from dipterous parasites).

22) *Cell provisioning.* Cell provisioning is of the facultative multiple type, i.e., there is a single large prey or up to 10 small prey, their number inversely proportional to their size (*alpestris, apicalis, ashmeadii, belfragei, clarconis, crassiformis, krombeini, mundus, pauxillus, pechumani, pompiliformis, punctifrons, similis, tarsatus, terminatus, texanus*). Only one prey per cell was found in 28 fully provisioned cells of *pechumani* and in most cells of *ashmeadii*.

23) *Orientation of prey in cell.* Most prey are deposited venter up in the cell, but orientation varies in *japonicus*, an Oriental acridid hunter. Mantid prey of the Old World species *albocinctus* and *costae* may be deposited on their back, venter, or side. Prey position varies in the Nearctic species *ashmeadii* (prey mainly venter up, but sometimes on side), *krombeini* (mainly venter up, but sometimes dorsum up), *pechumani* (venter up), *mundus* (dorsum up or venter up), and *terminatus* (mainly dorsum up).

24) *Position of egg on prey.* The egg is mainly deposited across the body just behind a forecoxa (*apicalis, belfragei, clarconis, crassiformis, krombeini, mundus, pauxillus, pechumani, psammobius, punctifrons, texanus*), but in the Old World mantid collectors it is placed on the outer margin of forecoxa (*costae*) or in front of the forecoxae (*albocinctus*). The position of the egg was not examined in the New World mantid collectors.

25) *Time of ovipositing.* In some species, oviposition takes place after the provisioning is completed, and in others after the first prey item is stored. Most authors dealing with North American species reported the size of the prey selected for oviposition, but not the time: the egg is deposited on a medium-size prey in *apicalis*, the largest or the second largest in *mundus*, the largest in *punctifrons* and *similis*, the largest in most *terminatus*, and the second largest in *psammobius* and *texanus*. It is known, however, that in a nest of *ashmeadii* the egg was laid on the last item put in the nest.

26) *Male burrows.* Males spend the night and inclement weather in burrows dug for that purpose (*similis, tarsatus, terminatus*) or probably (*apicalis*) use preexisting holes. The tumulus is not leveled. When resting inside, they stay close to the bottom and face the entrance. The burrow is closed off from inside (*similis, tarsatus, terminatus*). Male burrows were not studied in non-Nearctic species.

27) *Male perching behavior.* Male perching behavior was studied only in five species, all North American. Fights between males were frequent in *apicalis, similis*, and *terminatus*, rare in *tarsatus*, and they were not seen in *laevifrons*.

As can be seen, *Tachysphex* basically are ground nesters that dig their own nests (a few use galleries of other insects) and prey upon various orthopterans; the nest galleries do not branch. Their close relatives have basically the same habits, with a few striking modifications. *Holotachysphex* nest in plant stems and prey upon pyrgomorphid Acridoidea, a type of prey not observed in *Tachysphex* (Gess 1978, 1981). *Prosopigastra* use preexisting cavities and prey upon Heteroptera (summary in Pulawski 1979). Little is known about *Parapiagetia* (see Pulawski 1977*b*): one record of *mongolica* with a caterpillar prey, and one record of *longicornis* with an acridid. Nest gallery may branch in *Kohliella* (Gess 1980).

Geographic Distribution of Species.—The highest concentration of species is found in the southwestern United States (Fig. 3). The number of species in eastern North America is

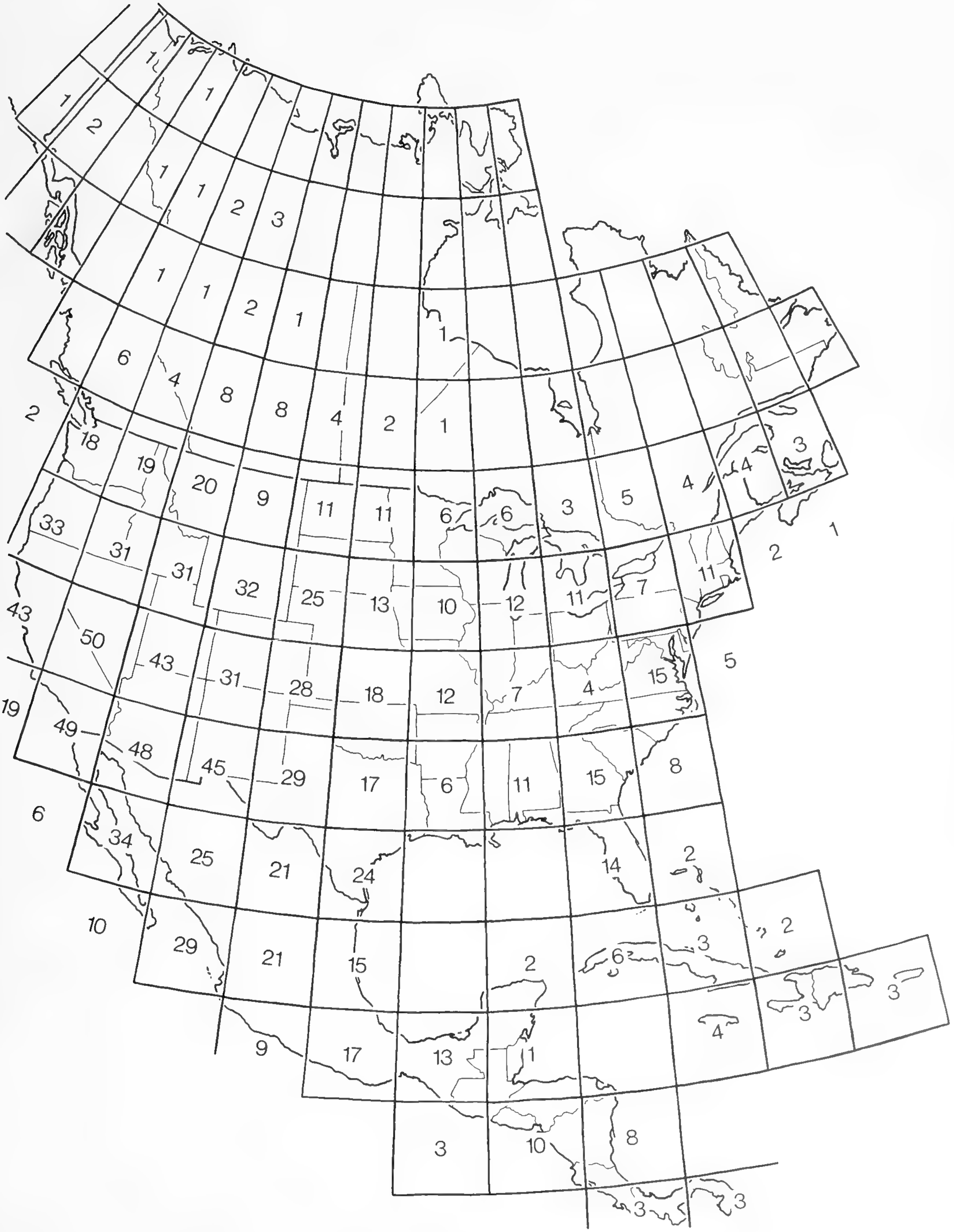

FIGURE 3. Number of species of *Tachysphex* in squares of 5 degrees of longitude and of latitude

much lower, although the area is equally well collected. I conclude that these numbers are proportional to the diversity of habitats (which is significantly greater in the western United States than in the eastern), and suggest that speciation in *Tachysphex* depends upon this diversity. The fact that more species of *Tachysphex* occur in the southwestern than the northwestern United States indicates that habitats with high temperatures and low humidity are best suited for most members of the genus.

The ranges of individual species differ longitudinally, latitudinally, and altitudinally, and apparently depend on ecological, historical, and populational factors. Some examples are discussed below.

1) Most North American species are endemic, but two (*pompiliformis* and *psammobius*) also occur in the Palearctic Region, and two species widely distributed in South America range into the southern United States (*iridipennis, ruficaudis*), and one (*inconspicuus*) to northern Mexico.

2) Relatively few species extend from Atlantic to Pacific coasts: *antennatus, apicalis, crassiformis, pompiliformis, semirufus* (only at the latitude of the Great Lakes), *tarsatus*, and *texanus*. The range of *aethiops* is similar, but the species has not been found between the Great Lakes and the Atlantic Coast. Most species are restricted to eastern (10 species) or to western North America (41 species). Remarkably, the western limits of the eastern species and the eastern limits of the western species do not coincide with any physical barriers (such as the Rocky Mountains). These limits must therefore depend upon some ecological factor, most likely humidity. Indeed, the relative humidity is markedly higher in the east than it is in the west (less than 20% in some areas in July), with the 60% line, for the April–July period, being close to the 100th meridian. The transcontinental species apparently tolerate various humidity levels.

3) *Tachysphex aethiops, pompiliformis*, and *semirufus* extend much farther south in the west (where they only occur in the mountains) than they do in the east (where they are found in lowlands). Apparently they are less tolerant of high temperatures than the other species.

4) *Tachysphex alpestris* has a more extensive north–south distribution than any other species (Alaska to Costa Rica). It occurs in a variety of habitats, from coastal beaches to high mountains. I interpret such a wide distribution as indication of wide tolerance of high and low temperatures and of high and low humidity. Another possibility, however, is that the microhabitats occupied by *alpestris* are all ecologically similar during its flight period.

5) Several pairs of closely related species have mutually exclusive ranges and different preferences for temperature and/or humidity (examples: *aequalis* and *mundus, alpestris* and *terminatus, antennatus* and *krombeini, laevifrons* and *tarsatus*). Most probably each pair had a common ancestor with a continuous geographic range. Subsequently the ranges became divided into an eastern and a western part (or southeastern and western), possibly during the Pleistocene; each population gradually differentiated morphologically and ecologically, and finally became isolated genetically. The western and southeastern forms of *apicalis* seem to be at an intermediate stage of such an isolation process. It is also possible that each member of a pair fills an ecological niche and makes it unavailable for the other.

6) The disjunct distribution of *pechumani*, which occurs only in southern New Jersey and the Lower Peninsula of Michigan, can be best explained by splitting of an initially continuous range during the Pleistocene glaciations, and the presence of some ecological barriers (perhaps absence of sandy soils) between the two parts of the extant range.

7) A type of distribution difficult to interpret is represented by *glabrior* which occurs from Central America to the Great Plains.

8) Three of the eight Caribbean species range widely on the adjacent continents, but have limited distributions on the islands (*apicalis* is known from two localities in eastern Cuba), *inconspicuus* from two localities in Jamaica, and *ruficaudis* from one locality in Jamaica). They probably are recent migrants to the area. Their migrations may have taken place during the Pleistocene, when the sea level dropped 130 m and greatly reduced the water barrier between Cuba and Florida on one side, and Jamaica and Central America on the other side. The remaining five species (*alayoi, antillarum, cubanus, dominicanus, quisqueyus*) probably evolved from ancestors that colonized the Caribbeans at an earlier time.

Classification of the Genus.—The present supraspecific classification was achieved by traditional taxonomic methods (study of characters, comparison of species, mental recognition of groups with unique characters or a unique combination of characters). This classification has several drawbacks, the most obvious being the heterogeneous nature of the *pompiliformis* group (which simply includes species lacking the diagnostic features of other groups and is not based on any synapomorphy). Clearly a worldwide cladistic analysis at the species group level in *Tachysphex* is imperative, but such an endeavor is beyond the scope of this regional revision, and will be attempted in a separate study. Therefore the traditional groups are used here.

De Beaumont was the first to subdivide *Tachysphex*. He used species groups rather than subgenera, recognizing seven such groups among the French species (1936), seven more (1940) in his revision of the Egyptian species (one subsequently became the genus *Holotachysphex*), and two additional groups in his other papers (1947*a, b*). The groups were based on characters such as the shape and length of the labrum and mouthparts, proportions of the vertex, shape of the gena (thick or thin) as seen from above, sculpture of the thorax, presence or absence of an episternal sulcus, shape of the propodeum, presence or absence of a median carina on sternum I, whether or not the hindtibial spur was modified, shape and sculpture of the female pygidial plate, presence or absence of a forefemoral notch in the male, and the type of sternal pilosity in the male. I found some of these characters unreliable at the species group level. I redefined (Pulawski 1971) all of de Beaumont's groups by adding some newly discovered characters (such as shape of the foretarsi, size of the jugal lobe, orientation of the veinlet cu-a in the hindwing), as well as using biological features (prey type). I combined some groups (e.g., *brullii, graecus*, and *obscuripennis* groups) and established one new group (the *euxinus* group). Subsequently, I also established three more groups (*mendozanus, terminatus, undatus*) in the South American fauna (Pulawski 1974*a*) and another (*nepharius*) in Australia (1977*a*). Menke (*in* Bohart and Menke 1976) in his review of *Tachysphex* kept the *brullii* and the *obscuripennis* groups separate based on prey.

I currently recognize the following 16 species groups:

albocinctus group of de Beaumont 1940 (xeric areas of world except North America).

brevipennis group of de Beaumont 1940 (South Africa to Mediterranean Basin, India, and Transcaspia), originally named the *imperfectus* group and renamed by Pulawski 1971.
brullii group of de Beaumont 1936 (cosmopolitan), originally named the *spoliatus* group (*spoliatus* is a junior synonym of *brullii*); includes the *obscuripennis* group of de Beaumont 1936 (originally named the *lativalvis* group but *lativalvis* is a junior synonym of *obscuripennis*) and the *graecus* group of de Beaumont 1947*b*).
erythropus group of de Beaumont 1936 (South Africa to Mediterranean Basin, India, and Transcaspia), originally named the *fluctuatus* group and renamed by Pulawski 1971.
euxinus group of Pulawski 1971 (Bulgaria to Lebanon, one species).
geniculatus group of de Beaumont 1940 (North Africa, Middle East), originally named the *luxuriosus* group and renamed by Pulawski 1971.
isis group of de Beaumont 1947*a* (Libya to Syria, one species).
julliani group of de Beaumont 1936 (South Africa to Mediterranean Basin, India, and Mongolia, New World).
mendozanus group of Pulawski 1974*a* (Argentina, one species).
nepharius group of Pulawski 1977*a* (Australia, one species).
panzeri group of de Beaumont 1936 (South Africa to central Europe, eastwards to India and Sri Lanka, China, and Mongolia).
plicosus group of de Beaumont 1936 (Africa to Mediterranean Basin, India, and Mongolia, two species), originally named *mediterraneus* group but renamed by Pulawski 1971.
pompiliformis group of de Beaumont 1936 (cosmopolitan), originally called the *pectinipes* group (*pectinipes* was a misdetermination of *pompiliformis*); includes the *nitidus* group of de Beaumont 1940 and the *speciosissimus* group of de Beaumont 1940.
schmiedeknechti group of de Beaumont 1940 (North Africa to Soviet Middle Asia, one species).
terminatus group of Pulawski 1974*a* (New World).
undatus group of Pulawski 1974*a* (South America).

Neither Afrotropical nor Oriental *Tachysphex* have been recently revised. Judging from my preliminary studies, all of the Oriental species belong to established species groups, whereas some Afrotropical species do not belong to any of them, and new groups will have to be recognized to accommodate them. Only four groups are represented in North and Central America (*pompiliformis, terminatus, brullii*, and *julliani* groups) and none is endemic.

Unsolved Taxonomic Problems.—According to de Beaumont (1960:14), "the genus *Tachysphex* seems to have been created in order to discourage taxonomists." Indeed, it is more difficult taxonomically than most sphecid genera because of individual and geographic variation, frequent absence of striking morphological differences between species, and large number of species. More specifically, I have been unable to understand or to place numerous North American specimens, in spite of strenuous efforts extending over a decade. A similar situation was reported by de Beaumont (1947*a*) in his study of Egyptian species. A source of frustration for the reviser, the leftover individuals probably fall into three main categories: (1) strongly aberrant individual variants, (2) cryptic species that lack easily observed diagnostic structures, and (3) single representatives of undescribed species with conspicuous diagnostic characters. Individuals that seemingly belong to the second category are common in certain areas, e.g., Sierra Nevada, California. With few exceptions, the undefined specimens are not described or discussed in the text below, and this makes the identification keys somewhat unreliable. Therefore, in order to assure maximum accuracy and to avoid confusion with leftover forms, each identification should be carefully checked against the description of the species.

Keys to the Species

The characters used in the keys require fresh material with well-preserved pilosity. Many specimens with worn setae, or a worn clypeus, cannot be determined to species.

♀♀[1]

1. Pygidial plate narrower; apical segments of gaster with thin preapical setae — 2
– Pygidial plate unusually broad (Fig. 147e); apical segments of gaster (Fig. 147c, d) with thick preapical setae (*julliani* group) — 4
2. Apicoventral margin of tarsomere V straight; claws not prehensile — 3
– Apicoventral margin of tarsomere V produced into lobe (Fig. 121d, 142e); claws prehensile (*brullii* group) — 5
3. Vertex with callosity (Fig. 114a) behind each hindocellus (*terminatus* group) — 20
– Vertex without callosities (*pompiliformis* group) — 28

julliani species group

4. Clypeal bevel roundly swollen throughout, not overhanging base of lip (Fig. 147a, b); vertex setae appressed or nearly so; propodeal side at most finely ridged — *coquilletti* Rohwer, p. 200
– Clypeal bevel ridgelike, overhanging base of lip (Fig. 150a, b); vertex setae erect; propodeal side distinctly ridged — *cockerellae* Rohwer, p. 204

brullii species group

5. Mid- and hindtarsomere IV shorter than wide, obtusely emarginate apically (Fig. 142d, 144c, 146b); claws short, stout; foretibial outer face with setae, without spines — 6
– Tarsomere IV as long as wide or longer (Fig. 121a), acutely emarginate (apex of emargination may be rounded); claws long, slender; foretibial outer face with setae and spines — 8
6. Mid- and hindtarsomere IV (Fig. 142a–d): apical emargination weakly obtuse, with exposed membrane, apicoventral margin not produced into lobe; hindfemur slender (Fig. 141d); rake spines of forebasitarsus 2–3× as long as basitarsal width; clypeal lip well defined (Fig. 141a), in vast majority of specimens with two lateral incisions on each side; vertex setae in most specimens 1.0–1.5 MOD long — *inconspicuus* (Kirby), p. 193
– Mid- and hindtarsomeres IV (Fig. 144c, 146b, c): apical emargination markedly obtuse, with membrane hidden,

[1] ♂♂: page 14.

apicoventral margin produced into lobe; hindfemur shorter, stouter (Fig. 144b); rake spines of forebasitarsus at most twice as long as width of basitarsus; clypeal lip ill defined, without lateral incisions (Fig. 144a, 146a); vertex setae slightly less to slightly more than 2.0 MOD long 7

7. Setae of propodeal dorsum inclined posterad; gaster black; hindcoxa without basal tooth; tergum V in most specimens densely punctate before apical depression; pygidial plate in many specimens densely setose apically; southern Texas to Tropic of Capricorn *iridipennis* (F. Smith), p. 196
– Setae of propodeal dorsum inclined anterad basomedially; gastral apex red; hindcoxa with basal tooth (see Fig. 141c); tergum V sparsely punctate before apical depression; pygidial plate sparsely setose; West Indies, Florida *alayoi* Pulawski, p. 198

8. Erect body setae woolly (Fig. 133b); setae 2.5–3.0 MOD long on lower gena, 2.0–2.5 MOD anterolaterally on scutum; scutal punctures many diameters apart; terga II–V (except laterally) without micropunctures *menkei* Pulawski, p. 184
– Erect body setae straight; setae 0.8–1.3 MOD long on lower gena, very short, appressed on scutum; midscutal punctures less than one diameter apart in most specimens (two to three diameters apart in *maurus* and some *aequalis*); terga densely micropunctate . . 9

9. Midscutal setae oriented laterad (except on midline); tarsomere V with one or two small spines on lateral margin, in most specimens also with central cluster of small spines on venter (Fig. 136b, c, 138) 10
– Scutal setae oriented posterad; tarsomere V without spines on lateral margin (spines present in most *aequalis*) or on venter 11

10. Pygidial plate densely setose throughout (Fig. 140) *cocopa* sp. n., p. 191
– Pygidial plate sparsely setose 11

11. Tarsomere V without basoventral spines (Fig. 136b) *acanthophorus* Pulawski, p. 187
– Tarsomere V with basoventral spines (Fig. 138) *armatus* Pulawski, p. 191

12. Propodeal dorsum: anterad-oriented setae covering a median area that extends from base to apex, thus posterad-oriented setae broadly separated; mesopleural punctures large . . . . . *maya* sp. n., p. 186
– Propodeal dorsum: anterad-oriented setae absent or present basomedially, posterad-oriented setae meeting apicomesally; mesopleural punctures fine to absent 13

13. Propodeal dorsum coarsely, irregularly rugose (Fig. 128b); side irregularly ridged *belfragei* (Cresson), p. 181
– Propodeal dorsum evenly microareolate (Fig. 120d, e); side at most finely ridged posteriorly 14

14. Clypeal lip broadened mesally (see Fig. 128a); mid- and hindfemora red (at least on apical third); central and southeastern United States *krombeiniellus* Pulawski, p. 181
– Clypeal lip not broadened (Fig. 120a); femora in most specimens black 15

15. Gaster black 16
– Gaster red, at least basally 18

16. Scutum shiny, punctures averaging more than one diameter apart; mesopleural punctures well defined, one to two diameters apart at middle; propodeal side in most specimens punctate; Arizona to Oklahoma, south to Costa Rica . . . . *maurus* Rohwer, p. 177
– Scutum dull, its punctures one diameter apart or less; mesopleural punctures inconspicuous, in most specimens less than one diameter apart, interspaces dull; propodeal side impunctate 17

17. Scutal hindcorner rounded (Fig. 120c); axilla evenly convex; east of Rocky Mountains *mundus* W. Fox (typical form), p. 169
– Scutal hindcorner prominent (see Fig. 125a); axilla steplike; New Jersey to Florida . . *utina* sp. n., p. 179

18. Mesopleural punctures at middle two to five diameters apart (Fig. 123a, b); posterolateral corner of scutum rounded (see Fig. 120c); west of Rocky Mountains to Mexico, eastern Wyoming . *aequalis* W. Fox, p. 172
– Mesopleural punctures at middle one diameter apart or slightly more, except in some *robustior* in which posterolateral corner of scutum is somewhat prominent (Fig. 125a); central Canada to Mexico . . . 19

19. Scutum slightly prominent posterolaterally (Fig. 125a); gaster red, or red basally and black apically; Kansas to Mexico . . . *robustior* Williams, p. 176
– Scutum rounded posterolaterally (Fig. 120c); gaster black apically; central Canada and United States . . *mundus* W. Fox (central United States and Canada form), p. 169

terminatus species group

20. Clypeal width 2.2× length (Fig. 118a, b); lip mesally with small, obtuse projection; frons shiny, with well-defined punctures (Fig. 118c) except in occasional western specimens . . *apicalis* W. Fox, p. 164
– Clypeus wider, except in *similis* in which clypeal lip has no mesal projection and frons is dull, evenly microsculptured to indistinctly punctate (Fig. 116a) . . 21

21. Mesopleural punctures several diameters apart; upper metapleuron with longitudinal carina (in some specimens with few longitudinal ridges) that starts beneath anterior end of flange and ends before propodeal spiracle (Fig. 109b); metapleural flange broad; Arizona and southern California to Argentina *ruficaudis* (Taschenberg), p. 149
– Mesopleural punctures less than to slightly more than one diameter apart (averaging up to two diameters apart in Bahamian specimens of *similis*); upper metapleuron different (see couplets 22–24 below), its flange narrow (*clarconis*) or broad . . . 22

22. Upper metapleuron with few simple ridges before propodeal spiracle; metapleural flange narrow, oblique carina beneath its anterior end vestigial or absent; gaster of many specimens all red; western North America *clarconis* Viereck, p. 147
– Upper metapleuron with prominence, lamella, or at least low carina (which is angulate posteriorly except in Caribbean species *antillarum*) before propodeal spiracle; metapleural flange broad, with oblique carina beneath its anterior end; gaster largely black (but all red in certain populations of *alpestris* and *linsleyi*) . . 23

23. Upper metapleuron with low carina (that is not angulate posteriorly) before propodeal spiracle; Caribbean Islands *antillarum* Pulawski, p. 149

– Upper metapleuron with prominence, lamella, or low carina that is angulate posteriorly; continental America and Bahamas ... 24

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– Prespiracular carina or prominence of upper metapleuron acutely angulate apically; oblique carina beneath anterior end of metapleural flange not expanding to outer margin of flange ... 25

25. Prespiracular prominence of upper metapleuron low, obtusely angulate in lateral view, its anterior margin markedly longer than the posterior margin (Fig. 111b–d) *alpestris* Rohwer, p. 151

– Prespiracular prominence of upper metapleuron large, toothlike, its anterior and posterior margins about equal in length (Fig. 114b–d, 116b–d) ... 26

26. Clypeal integument hidden by vestiture (except anteriorly); frons in most specimens with well-defined punctures; vertex width 2.0–2.2 × length; anterolateral scutal setae about 2.0 MOD long; prespiracular prominence of upper metapleuron broad (Fig. 114b–d) *terminatus* (F. Smith), p. 156

– Clypeal integument not hidden by vestiture; frontal punctures conspicuous (*quisqueyus*) or ill defined (*similis*); vertex width : length ratio 1.4–1.7 in *similis*, 1.6–2.0 in *quisqueyus*; prespiracular prominence of upper metapleuron narrow (Fig. 116b–d) in some specimens; anterolateral scutal setae 1.0–1.3 MOD long ... 27

27. Frons with well-defined punctures; prespiracular prominence of upper metapleuron broad (see Fig. 114b–d); Hispaniola ... *quisqueyus* sp. n., p. 156

– Frons with ill-defined punctures; prespiracular prominence of upper metapleuron narrow in many specimens (Fig. 116b–d); continental North America and Bahamas *similis* Rohwer, p. 161

pompiliformis species group

28. Subalar fossa carinate below; upper mesopleuron longitudinally ridged; postspiracular carina unusually long (Fig. 16a, b) ... *punctifrons* W. Fox, p. 37

– Subalar fossa not carinate below; mesopleuron not ridged; postspiracular carina shorter (except in *acutus*) ... 29

29. Midscutal setae oriented radially, forming a rosettelike pattern (Fig. 105d, e); axilla of usual shape; labrum convex and protruding beyond clypeus (Fig. 105b, c) in nearly all specimens; sternum I without apical depression; basal platform of sternum II acutely angulate *ashmeadii* W. Fox, p. 141

– Midscutal setae oriented longitudinally to transversely, but not radially; if radially then with following characters: basal plate of sternum II at least weakly biemarginate (*opata*), or clypeal lobe unusually broad (*crassiformis* and *pinal*, Fig. 48a, 52a), or axilla expanded (*crassiformis*, Fig. 48b, d, e), or sternum I with apical depression (*yolo*, compare Fig. 91c, d); labrum flat, in many specimens not protruding beyond clypeus ... 30

30. Hypostomal carina lamelliform (greatest height equal to about ⅔ of basal width of mandible); setae near hypostomal carina equal to about 0.5 of basal width of mandible; axilla expanded or steplike ... *paiute*, p. 80

– Hypostomal carina not broadened (except in *lamellatus*); setae near hypostomal carina shorter (except in *idiotrichus*); axilla not expanded or steplike (except in most *crassiformis*) ... 31

31. Clypeal lip markedly sinuate (Fig. 83a); midscutal setae oriented transversely, forming characteristic pattern (see Fig. 90b, c); punctures many diameters apart laterally and posteriorly to pattern; mesopleural punctures well defined; hindlegs largely red ... *oasicola* sp. n., p. 113

– Clypeal lip differently shaped; scutal setae oriented uniformly posterad; and/or scutum closely punctate; and/or mesopleuron impunctate, and/or legs black 32

32. Sternum I apicomesally with horizontal depression (Fig. 91c, d) or gradually sloping posterad (Fig. 84b); midscutal setae oriented transversely (posterolaterally in *sonorensis*, some *tsil*, and most *yuma*); mesopleuron punctate (punctures evanescent in some *yolo*) ... 33

– Different combination of characters: sternum I apicomesally at most with shallow, ill-defined depression; midscutal setae oriented longitudinally to transversely (radially in some *crassiformis*, some *pinal*, and most *opata*); mesopleuron punctate or impunctate 41

33. Clypeal lip undulate or with obtuse, median projection (Fig. 95a, 97a) ... 34

– Clypeal lip arcuate or sinuate, weakly undulate in some *sonorensis* 35

34. Clypeal lip undulate (Fig. 97a); hypostomal carina in many specimens lamelliform (Fig. 97c) *lamellatus* Pulawski, p. 130

– Clypeal lip undulate or with obtuse, median projection (Fig. 95a); hypostomal carina not lamelliform *arizonae* Pulawski, p. 129

35. Sternum I gradually sloping apically (Fig. 84b; body length 11–13 mm ... *amplus* W. Fox, p. 115

– Sternum I with horizontal depression apically (Fig. 91c, d); body length 6.5–11.0 mm ... 36

36. Dense clypeal punctation attaining base of lip laterally, thus bevel not extending laterad to lip corner (Fig. 86a, b) ... *yolo* Pulawski, p. 117

– Dense clypeal punctation not attaining base of lip laterally, thus bevel extending laterad to lip corner 37

37. Ridges of propodeal side absent anteriorly (Fig. 88b), or fine anteriorly and coarse posteriorly; length of flagellomere IV 3.6–4.2 × width ... *yuma* Pulawski, p. 120

– Propodeal side uniformly ridged; length of flagellomere IV up to 3.2 × width 38

38. Mesopleuron beneath scrobe: punctures averaging more than one diameter apart (Fig. 101a, b), setae nearly appressed to nearly erect; scutal setae nearly erect anterolaterally 39

– Mesopleuron beneath scrobe: punctures averaging less than one diameter apart (Fig. 91a, b), setae appressed; scutal setae nearly appressed anterolaterally 40

39. Length 8.0–8.5 mm; Arizona and Mexico (Veracruz and Jalisco states) *tsil* sp. n., p. 131

– Length 9–11 mm; North Dakota and Oregon to Costa Rica *sonorensis* (Cameron), p. 133

40. Clypeal lobe arcuate (Fig. 90a); length of flagellomere I

1.9–2.2× apical width in eastern and 2.2–2.4× in western populations; body length 7.5–10.5 mm; United States to central Mexico, transcontinental
texanus (Cresson), p. 121

– Clypeal lobe sinuate (Fig. 93a); length of flagellomere I 1.9–2.1× apical width; northwestern Nebraska, Arizona, California, Mexico ... *huchiti* sp. n., p. 126

41. Setae erect on scape, vertex (Fig. 55b) and scutum, 2.5–3.0 MOD long on vertex, about 2.0 MOD long on scutum anteriorly; mesopleuron dull, with inconspicuous punctures; sterna III–V with graduli; southwestern Texas to southern California, also Mexico (Jalisco)
idiotrichus Pulawski, p. 85

– Setae appressed or nearly so on scape, appressed or shorter than 1.0 MOD on scutum, no longer than 1.5 MOD on vertex (up to 2.0 MOD long on vertex and scutum in some populations of *psammobius* in which mesopleuron is glossy, coarsely punctate); sterna without graduli 42

42. Metapleuron with oblique carina or lamella emerging from anterior end of flange; flange broadened (Fig. 103d); terga I and II unsculptured apically (Fig. 103e); malar space present (Fig. 103b) 43

– Metapleuron without oblique carina beneath flange; flange not broadened except in some *crassiformis* in which terga I and II are sculptured from base to hindmargin; malar space absent 44

43. Metapleuron with single carina starting beneath anterior end of flange and ending before propodeal spiracle; propodeal side not ridged; setae of propodeal dorsum inclined posterad on broad, basal zone that extends from spiracle to spiracle; hindcoxa not carinate; flagellum partly brown or red; forewing with dark, transverse fascia
psilocerus Kohl, p. 139

– Metapleuron with oblique lamella emerging from anterior end of flange, and with one or two longitudinal carinae behind lamella (Fig. 103c, d); propodeal side ridged; setae of propodeal dorsum inclined anterad from base to apex except for a few basomedian setae that are inclined posterad; hindcoxa carinate; flagellum black; forewing uniformly colored *scopaeus* sp. n., p. 137

44. Terga I and II unsculptured and glabrous apicomesally; setae of midfemoral venter erect, sparse; flagellum largely brown or red; mespleuron with well-defined punctures
papago Pulawski, p. 137

– Terga I and II microsculptured and setose from base to hindmargin except in some species in which mesopleuron is impunctate; setae of midfemoral venter appressed or (*psammobius*) erect, dense; flagellum black (except largely red in *pechumani* in which mesopleuron is impunctate)
45

45. Mesopleuron with fine, well-defined punctures, and propodeal side unridged or with microscopic ridges; midscutal setae of most specimens oriented radially, forming rosette-like pattern (see Fig. 105d, e) or (some specimens) midline setae of rosette oriented posterad (see Fig. 90c); basal platform of sternum II in most specimens biemarginate apically (Fig. 75b, c); distance between corners of clypeal lobe about 1.5× clypeal length)
opata sp. n., p. 106

– Mesopleuron or propodeal side differently sculptured (propodeal side ridged in many specimens); midscutal setae oriented longitudinally or transversely, but radially in some *crassiformis* and some *pinal* (in which distance between clypeal lip corners is 1.7–2.0× clypeal length) (Fig. 48a, 52a); basal platform of sternum II acutely angulate to rounded apically, but biemarginate in some *pinal* 46

46. Mesopleuron with well-defined punctures, and either clypeal lip with two lateral incisions or vertex setae 1.1–1.5 MOD long; propodeal side ridged 47

– Mesopleuron differently sculptured; if punctate then either clypeal lip with one lateral incision or not incised, or vertex setae shorter; propodeal side unridged in many specimens 49

47. Clypeal lip with two incisions laterally (Fig. 81a); setae 0.3–0.6 MOD long on vertex *glabrior* Williams, p. 112

– Clypeal lip not incised laterally; setae 1.1–1.5 MOD long on vertex 48

48. Clypeal lip projected mesally (Fig. 77a), bevel in many specimens anteriorly flat or barely concave; body length 8.6–11.0 mm; gaster black *hurdi* R. Bohart, p. 108

– Clypeal lip not projected mesally (Fig. 79a), bevel evenly convex; body length 6–7 mm; gaster red to black
psammobius Kohl, p. 109

49. Flagellum largely red; clypeus and frons with brassy golden vestiture; Michigan and New Jersey
pechumani Krombein, p. 50

– Flagellum black; vestiture of clypeus and frons silvery, with golden tinge in some specimens, brassy golden in *bohartorum* (western United States) 50

50. Setae of mesothoracic venter unusually dense (Fig. 59b); in most specimens clypeal lip emarginate (Fig. 59a) and hindfemur and hindtibia red
musciventris Pulawski, p. 88

– Setae of mesothoracic venter usual; clypeal lip not emarginate and/or hindleg black 51

51. Lateral setae of propodeal dorsum oriented posterad, joining apicomesally; propodeal side alutaceous, shiny, with minute punctures (Fig. 65b)
apricus Pulawski, p. 94

– Lateral setae of propodeal dorsum oriented anterad to laterad, or erect; propodeal side in most species differently sculptured (microareolate, microridged, rugose, or ridged) 52

52. Mesopleuron angulate or weakly carinate between dorsal end of postspiracular carina and anterior end of subalar carina (Fig. 14b); basal half of sternum I with broad, longitudinal keel (Fig. 14c); east of 100th meridian
acutus Patton, p. 34

– Mesopleuron not angulate or carinate between postspiracular carina and subalar carina; sternum I at most with longitudinal carina 53

53. Clypeal lip arcuate, with two incisions laterally (Fig. 73a); mesopleuron and propodeal side uniformly microareolate, impunctate, propodeal hindface contrastingly ridged; hindcoxa with expanded carina basally; pygidial plate broader apically (Fig. 73c) *verticalis* Pulawski, p. 104

– Clypeal lip with one lateral incision or not incised (two incisions laterally in *crenulatus* and *spatulifer* in which hindcoxal carina, if present basally, is not expanded);

mesopleuron and/or propodeum in most specimens differently sculptured; pygidial plate narrower 54

54. Fore- and midfemoral venter with large, sparse punctures, without micropunctation (Fig. 8c, d); vertex setae about 0.6 MOD long anteriorly and 0.3 MOD long posteriorly; wings strongly infumate; pygidial plate of most specimens punctatorugose (Fig. 8b) .... *aethiops* (Cresson), p. 26
– Fore- and midfemoral venter densely micropunctate; or (*mirandus, tipai*) sparsely punctate and without micropunctures, but then vertex setae erect, about 1.0 MOD long and wings hyaline to moderately infumate; pygidial plate alutaceous or punctate 55
55. Forecoxa with apical process (Fig. 25b, c, 29b, c); tarsomeres IV and V elongate (Fig. 25d, e, 29d, e); femora and tibiae black 56
– Forecoxa without apical process and/or tarsomeres IV and V not elongate or (*occidentalis*) hindfemur and hindtibia all or partly red 57
56. Clypeus and frons with brassy golden vestiture; clypeal lip deeply incised laterally (Fig. 29a) .... *bohartorum* Pulawski, p. 51
– Clypeus and frons with silvery vestiture; clypeal lip shallowly incised laterally (Fig. 25a) .... *hopi* sp. n., p. 47
57. Mesopleuron coarsely punctatorugose or rugose; trochanteral venter sparsely punctate in most specimens .... *irregularis* Pulawski, p. 55
– Mesopleuron finely sculptured (microareolate to finely punctate); if finely rugose (many *powelli*) then trochanteral venter densely punctate 58
58. Clypeal lip with several shallow concavities (Fig. 39b, 41b), its free margin dentate or undulate (Fig. 39a, 41a) or (some *spatulifer*) with obtuse projection mesally 59
– Clypeal lip flat or (some specimens) with a few vestigial concavities, its free margin arcuate or obtusely angulate 60
59. Clypeal lip obtusely prominent mesally (Fig. 39a); trochanteral venter densely punctate .... *spatulifer* Pulawski, p. 63
– Clypeal lip emarginate mesally (Fig. 41a), emargination flanked by obtuse projection (emargination rudimentary or absent in some individuals); mid- and hindtrochanteral venter sparsely punctate .... *crenulatus* W. Fox, p. 65
60. Terga II–IV glabrous (except laterally), nonfasciate apically; fore- and midfemoral venter sparsely punctate, without micropunctation; basal platform of sternum II broad apically .... *mirandus* Pulawski, p. 102
– Terga II–IV finely setose throughout; if glabrous (some *semirufus*) then fore- and midfemoral venter densely punctate (setae inconspicuous in some *tipai* in which basal platform of sternum II is angulate apically) 61
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– Punctures of mesothoracic venter no more than one diameter apart and/or flagellomere II shorter; basomedian setae of propodeal dorsum oriented posterad or (*semirufus*) all setae erect 62
62. Hindfemur and hindtibia all or partly red; clypeal lip evenly arcuate, not incised laterally (Fig. 61a, 63a); propodeal side unridged or with microscopic ridges when seen from certain angles 63
– Hindfemur and hindtibia in most specimens black; if red (some *antennatus*, some *crassiformis*) then clypeal lip incised laterally and propodeal side in most specimens ridged 64
63. Humeral plate of forewing uniformly yellowish, contrasting with dark median plate; mesopleuron minutely punctate, but mesopleural vestiture largely concealing integument; most setae of propodeal dorsum oriented transversely .... *solaris* Pulawski, p. 93
– Humeral plate of forewing yellowish anteriorly and dark posteriorly, not contrasting with median plate; mesopleuron impunctate, mesopleural vestiture not concealing integument; most setae of propodeal dorsum oriented anterolaterad .... *occidentalis* Pulawski, p. 91
64. Sternum II uniformly micropunctate and setose from base to apex; mesopleuron and propodeal side and hindface uniformly densely microareolate; middle clypeal section of many specimens densely punctate from frontoclypeal suture to lip (Fig. 33a); mesopleural setae appressed *laevifrons* (F. Smith), p. 56
– Sternum II impunctate and glabrous on apical depression; mesopleuron differently sculptured from propodeal side and/or hindface; clypeus with sparsely punctate bevel; mesopleural setae appressed to erect 65
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– Setae of propodeal dorsum erect or inclined anterad in lateral view, no longer than 0.7 MOD; terga of many specimens fasciate 66
66. Mesopleuron with fine but conspicuous microsculpture, with minute, sparse punctures (Fig. 21c, 50b) 67
– Mesopleuron without conspicuous microsculpture, its punctures larger and/or denser, or mesopleuron impunctate, punctatorugose, or (many *powelli*) slightly rugose 69
67. Vertex width 1.6–1.8× length; gena thick in dorsal view (Fig. 21b); setae below mesopleural scrobe markedly shorter than MOD; terga not fasciate; western North America .... *pauxillus* W. Fox, p. 42
– Vertex width 0.9–1.0× length; gena thin in dorsal view; setae below mesopleural scrobe about 1.0 MOD long; terga I–IV fasciate apically; Caribbean Islands 68
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– Trochanteral venter closely punctate to impunctate; if impunctate, then vertex narrower and/or clypeal lip not incised laterally, or (*orestes*) setae of postocellar impres-

sion 0.5 MOD long or less and silvery tergal fasciae well defined . . . 70

70. Clypeal lip obtusely triangular mesally (Fig. 12a) . . . *angelicus* sp. n., p. 33
– Clypeal lip not triangular mesally . . . 71
71. Fore- and midfemoral venter micropunctate and also with large, sparse punctures (Fig. 6b, c) . . . *montanus* (Cresson), p. 25
– Fore- and midfemoral venter densely micropunctate, at most with a few large punctures basally . . . 72
72. Setae erect or nearly so on mesopleuron, erect on vertex . . . *powelli* R. Bohart, p. 38
– Setae inclined posterad or appressed on mesopleuron, appressed to erect on vertex . . . 73
73. Hypoepimeral setae appressed or nearly so (Fig. 34b), inclined adjacent to subalar fossa in some individuals; clypeal lobe (Fig. 34a) of usual width (distance between lip corners 1.4–1.6 × clypeal length); axilla simple; gaster all or partly red, but all black in some specimens from Pacific Coast . . . 74
– Hypoepimeral setae inclined to erect, but if appressed (many *antennatus*, many *crassiformis*), then distance between clypeal lip corners 1.7–2.5 × clypeal length, and axilla steplike or expanded in most *crassiformis*, or (many *krombeini*) gaster all black and occurring in southeastern United States . . . 75
74. Transcontinental . . . *tarsatus* (Say), p. 57
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– Pygidial plate at most weakly alutaceous; gaster in most specimens all or partly red . . . 76
76. Clypeal lobe broad (distance between its corners 1.7–1.9 × clypeal length, as on Fig. 52a and 54a); vertex setae erect, about 1.0 MOD long; clypeal lobe arcuate (Fig. 52a, 54a) . . . 77
– Clypeal lobe narrower, or vertex setae appressed or nearly so, or (*tahoe*) clypeal lip slightly sinuate (Fig. 57a) . . . 78
77. Vertex width 1.3–1.5 × length; gaster black basally, red apically; central Mexico . . . *toltec* sp. n., p. 83
– Vertex width 1.0–1.1 × length; gaster red; California and New Mexico to Sonora, Mexico . . . *pinal* sp. n., p. 81
78. Free margin of clypeal lobe weakly arcuate or sinuate, nearly straight; lobe in most specimens unusually broad (Fig. 46a, 48a), width 1.8–2.5 × clypeal length (1.7 × in some *crassiformis* but then axilla expanded); propodeal dorsum not sloping or scarcely sloping toward transverse carina that separates it from hindface (sloping just above median groove of hindface); carina well defined at least mesally . . . 79
– Free margin of clypeal lobe arcuate, sinuate, or shallowly emarginate; lobe width 1.4–1.7 × clypeal length; axilla simple; propodeal dorsum sloping toward transverse carina that separates it from hindface (carina evanescent in many specimens) . . . 80
79. Axilla in most specimens expanded into lobe which may be large (overhanging lateral fossa) or small, steplike (Fig. 48b–e); mesopleural setae partly hiding integument, averaging about 0.8 MOD just below scrobe; setae of propodeal dorsum oriented anterad along midline (only a few such setae present in some individuals) . . . *crassiformis* Viereck, p. 75
– Axilla not expanded; setae either shorter and not concealing sculpture on mesopleuron or oriented anterolaterad on propodeal dorsum (parted mesally) . . . *antennatus* W. Fox, p. 72
80. Clypeal lip evenly arcuate, not incised laterally (Fig. 43a); setae appressed on vertex and along hypostomal carina; foretarsomere I with 3–6 rake spines (no more than 3 apical spines with confluent or contiguous basal fossae), foretarsomere II with 2–4 rake spines (Fig. 43b); body length 5.0–7.5 mm . . . *miwok* sp. n., p. 67
– Clypeal lip sinuate or incised laterally, and/or body length over 7.5 mm (6.5–11.0 mm); setae appressed to erect on vertex, suberect to erect along hypostomal carina; foretarsomere I and II of many specimens with more than 6 and 4 rake spines, respectively; body length 6.5–11.0 mm . . . 81
81. Clypeal lip not incised laterally (Fig. 67a); setae appressed or nearly so on vertex, erect and 1.3 MOD long along hypostomal carina posteriorly, almost erect on hypoepimeral area, and appressed below mesopleural scrobe; mandibular outer face in most specimens with longitudinal sulcus beyond notch (Fig. 67c, d) . . . *sulcatus* sp. n., p. 97
– Clypeal lip in many specimens incised laterally; setae different; mandibular outer face without sulcus or with rudimentary sulcus . . . 82
82. Clypeal lip weakly sinuate, not incised laterally (Fig. 57a); vertex setae erect; body length 6.5–8.0 mm . . . *tahoe* sp. n., p. 86
– Clypeal lip not sinuate, incised laterally in most specimens; vertex setae appressed to erect; body length 7–11 mm . . . 83
83. Gaster red basally, black apically or (some specimens) all black . . . *pompiliformis* (Panzer), p. 20
– Gaster all red . . . 83
84. Clypeal lip emarginate mesally; mandibular ventral margin convex basally; trochanteral venter shiny, in most specimens sparsely punctate or impunctate . . . *orestes* sp. n., p. 31
– Clypeal lip not emarginate mesally; mandibular ventral margin straight or concave basally; trochanteral venter sparsely to densely punctate . . . undescribed species and/or red phase of *pompiliformis*

♂♂

(*Tachysphex orestes* not included)

1. Vertex width less than length; distance between clypeal lobe corner and orbit about twice distance between corners (Fig. 148a); sterna IV–VI all or largely asetose; forefemoral notch margined anteriorly and posteriorly (Fig. 148c, d, 150c), its surface slightly raised above adjacent area (*julliani* group) . . . 3
– Vertex width equal to length or more, or clypeal lobe broader; sterna IV–VI densely setose (but largely asetose

in *alayoi, iridipennis, menkei,* and *mirandus*); forefemoral notch in most species not margined 2

2. Vertex with callosity behind each hindocellus (Fig. 114a); if callosities indistinct (some *clarconis*), then vertex width more than twice length and foretarsal rake present; setae of propodeal dorsum inclined anterad (*terminatus* group) 4
– Vertex without callosities or, if callosities present (some *iridipennis*), setae of propodeal dorsum slightly inclined posterad; vertex width less than twice length and/or foretarsal rake absent (*brullii* and *pompiliformis* groups) 12

julliani species group

3. Vertex setae appressed or nearly so; propodeal side unridged or finely ridged posteriorly; gastral apex brown .... *coquilletti* Rohwer, p. 200
– Vertex setae erect; propodeal side ridged, ridges rarely evanescent; gaster red, exceptionally black apically *cockerellae* Rohwer, p. 204

terminatus species group

4. Forefemur entire; Caribbean Islands 5
– Forefemur notched; continental America and Bahamas 6
5. Upper metapleuron with longitudinal carina that starts at about midlength of flange and ends before propodeal spiracle .... *antillarum* Pulawski, p. 149
– Upper metapleuron with toothlike, prespiracular prominence (see Fig. 114b–d) .... *quisqueyus* sp. n., p. 156
6. Foretarsal rake absent and clypeus broad (width 3.2–3.6× length); upper metapleuron with longitudinal carina (with few longitudinal ridges in some specimens) that starts beneath anterior end of flange and ends before propodeal spiracle (Fig. 109b); metapleural flange broad; Arizona and southern California to Argentina .... *ruficaudis* (Taschenberg), p. 149
– Foretarsal rake present; if absent (most *apicalis*), then clypeus narrow (width 2.1–2.3× length) or (some *linsleyi*) upper metapleuron distinctive (Fig. 112a–c) 7
7. Foretarsal rake absent; if present (some southeastern specimens), then propodeum strongly sculptured between dorsum and side (Fig. 118e); clypeal width 2.0–2.3× length .... *apicalis* W. Fox, p. 164
– Foretarsal rake present; if absent (some *linsleyi*), then upper metapleuron distinctive (Fig. 112a–c); propodeum finely sculptured between dorsum and side; clypeus broader (except in *alpestris* and *similis*) 8
8. Upper metapleuron with few simple ridges before propodeal spiracle; metapleural flange narrow, oblique carina beneath its anterior end vestigial or absent; graduli shallow, not invaginated; gaster red or black *clarconis* Viereck, p. 147
– Upper metapleuron with prominence, lamella, or at least a low carina (which is angulate posteriorly) in front of propodeal spiracle; metapleural flange broad, with oblique carina beneath its anterior end; graduli deeply invaginated (except apically) underneath basal, triangular area in front of them; gaster in most specimens black (red in certain populations of *alpestris*) 9
9. Prespiracular prominence of upper metapleuron rounded apically, funnel-shaped (Fig. 112a–c); oblique carina beneath anterior end of metapleural flange as high as flange or nearly so .... *linsleyi* R. Bohart, p. 153
– Prespiracular carina or prominence of upper metapleuron acutely angulate at apex; oblique carina beneath anterior end of metapleural flange lower than flange 10
10. Prespiracular prominence of upper metapleuron low, obtusely angulate (Fig. 111b–d), its anterior margin markedly longer than the posterior .... *alpestris* Rohwer, p. 151
– Prespiracular prominence of upper metapleuron large, toothlike, its anterior and posterior margins about equal in length (Fig. 114b–d, 116b–d) 11
11. Scutal setae about 1.3 MOD long anterolaterally; sculpture not totally obscured by vestiture between antennal socket and orbit; frons in most specimens with ill-defined punctures; vertex width 1.6–2.2× length *similis* Rohwer, p. 161
– Scutal setae about 2.0 MOD long anterolaterally; sculpture in most specimens obscured by vestiture between antennal socket and orbit; frons in most specimens with well-defined punctures; vertex width 2.0–2.5× length *terminatus* (F. Smith), p. 156

brullii and *pompiliformis* species groups

12. Setae of propodeal dorsum inclined posterad, or median setae oriented anterad while lateral setae oriented posterad and joining apicomesally; or setae erect and mesopleural punctures well defined 13
– Setae of propodeal dorsum inclined anterad, anterolaterad, or laterad; or (*maya*) posteriorly oriented setae broadly separated and not joining apicomesally, or setae erect and mesopleuron impunctate 27
13. Sterna simple; forefemoral notch of most specimens compressed, its glabrous bottom crestlike (Fig. 65e) *apricus* Pulawski, p. 94
– Sterna III–V with graduli or transverse sulcus; forefemoral notch not compressed, its bottom not crestlike 14
14. Propodeal dorsum longitudinally ridged or irregularly rugose (Fig. 128b, 141b), at least basally 15
– Propodeal dorsum evenly microreticulate (Fig. 120d, e) 18
15. Vertex width less than length; setae appressed on vertex and scutum; mesopleural punctures less than one diameter apart; tibiae red .... *belfragei* (Cresson), p. 180
– Vertex width more than length; setae erect on vertex and scutum, at least 1.0 MOD long; mesopleural punctures one diameter or more apart, at least posteriorly; tibiae black or (*alayoi*) partly red 16
16. Setae of propodeal dorsum inclined anterad on basomedian area; propodeal side with well-defined ridges; hindcoxa with basal tooth; gastral apex red in most specimens; West Indies, Florida .... *alayoi* Pulawski, p. 198
– Setae of propodeal dorsum erect or inclined obliquely posterad; propodeal side not ridged; if ridged (*iridipennis*) then hindcoxa without basal tooth; gaster black 17
17. Clypeal lobe: distance between corners less than distance between corner and orbit (Fig. 144e); scutal setae 2.0 MOD long; propodeal side ridged (ridges probably eva-

nescent in some specimens); sterna III–VI sparsely punctate; hindcoxa without basal tooth *iridipennis* (F. Smith), p. 196

– Clypeal lobe: distance between corners at least equal to distance between corner and orbit (Fig. 141e); scutal setae 1.0–1.2 MOD long; propodeal side at most partly ridged; sternal punctures nearly contiguous; hindcoxa with basal tooth (Fig. 141c) *inconspicuus* (Kirby), p. 193

18. Setae 1.6–2.5 MOD long on lower gena and anterolaterally on scutum; sterna III–VI impunctate, glabrous; scutal and mesopleural punctures several diameters apart *menkei* Pulawski, p. 184

– Setae 0.5–0.8 MOD long on lower gena, very short and appressed (or nearly so) on scutum; sterna punctate and pubescent throughout; in most specimens scutal and mesopleural punctures less than one diameter apart 19

19. Clypeal vestiture totally concealing sculpture (except on lip); midscutal setae oriented laterad (except on midline); sterna III–VI (except laterally) with straight transverse sulcus (which is visible only when segments are fully extended) 20

– Clypeal integument easily visible on bevel; scutal setae oriented posterad; sterna III–VI with graduli 22

20. Mesopleural vestiture not concealing sculpture; sternum II flat *armatus* Pulawski, p. 191

– Mesopleural vestiture partly concealing sculpture; sternum II somewhat swollen along foremargin of apical depression (morphologically indistinguishable males of two species) 21

21. Northern half of Mexico north to Texas, Colorado, Utah, Nevada, and California *acanthophorus* Pulawski, p. 187

– Known from southeastern California, Arizona, and Sonora, Mexico *cocopa* sp. n., p. 191

22. Tibiae red 23

– Tibiae all or largely black 24

23. Penis valve: Figure 131a, b; vertex setae appressed; mesopleural vestiture golden in fresh specimens; hindfemur red in apical third; gaster red basally *krombeiniellus* Pulawski, p. 181

– Penis valve: Figure 121g, h; vertex setae erect or inclined (at least partly); mesopleural vestiture silvery; hindfemur black; gaster all black or basally red *mundus* W. Fox, p. 169

24. Setae of sterna IV–VI extending beyond sternal hindmargin and forming short apical fasciae (Fig. 125c) *robustior* Williams, p. 176

– Sterna without apical, setal fasciae 25

25. Gaster red basally; frontal vestiture golden or (some specimens) silvery; clypeal lobe: distance between corners equal to about 1.25 of clypeal length (Fig. 123c); British Columbia to Chiapas, in United States west of the 103rd meridian *aequalis* W. Fox, p. 172

– Gaster black; frontal vestiture silvery; clypeal lobe: distance between corners equal to 1.0–1.25 of clypeal length; east of the Rocky Mountains 26

26. Midscutal punctures less than one diameter apart; axilla steplike, overhanging lateral (subvertical) portion *utina* sp. n., p. 179

– Midscutal punctures more than one diameter apart (most specimens) to slightly less than one diameter apart; axilla not steplike *maurus* Rohwer, p. 177

27. Subalar fossa carinate below (Fig. 16a, b); upper mesopleuron longitudinally ridged; postspiracular carina unusually long; east of Rocky Mountains, also Idaho *punctifrons* W. Fox, p. 37

– Subalar fossa not carinate below; mesopleuron not ridged; postspiracular carina shorter (except in *acutus*) 28

28. Midscutal setae oriented radially, forming a rosettelike pattern (Fig. 105d, e); clypeal free margin shallowly concave between lobe and orbit (Fig. 105f) and distance between lip corners about 1.3× clypeal length; labrum convex and protruding beyond clypeus in nearly all specimens (Fig. 105b, c); axilla of usual shape; sternum I without apical depression, basal plate of sternum II angulate; sterna III–VI with well-defined graduli that delimit a triangular area (graduli visible only when sterna are fully extended) *ashmeadii* W. Fox, p. 141

– Midscutal setae oriented longitudinally to transversely, but not radially; if radially, then with following characters: clypeal free margin deeply concave between lobe and orbit, basal plate of sternum II rounded or biemarginate, and graduli absent (*opata*), or distance between clypeal lobe corners is 1.5–1.6× clypeal length (*crassiformis* and *pinal*), or axilla expanded (*crassiformis*), or sternum I with an apical depression and graduli absent (*yolo*); labrum flat, in most specimens not protruding beyond clypeus 29

29. Hypostomal carina lamelliform, its greatest height equal to about ⅔ of basal width of mandible; setae near hypostomal carina equal to about 0.5 of basal width of mandible; axilla expanded or steplike; clypeal lobe broad, its free margin nearly straight (Fig. 51b) *paiute* sp. n., p. 80

– Hypostomal carina not lamelliform (except in *lamellatus*); setae near hypostomal carina shorter (except *idiotrichus*); axilla not expanded or steplike except in most *crassiformis*; clypeal lobe in most species differently shaped 30

30. Clypeal lip sinuate (Fig. 83b); midscutal setae oriented transversely, forming characteristic pattern (see Fig. 90c); punctures several diameters apart laterally and posteriorly to pattern; mesopleural punctures well defined *oasicola* sp. n., p. 113

– Clypeal lip differently shaped, and/or scutal setae oriented posterad, and/or scutal punctures close to each other, and/or mesopleuron impunctate 31

31. Sternum I apicomesally with horizontal depression (Fig. 91c, d), or gradually sloping posterad (Fig. 84b); midscutal setae oriented transversely (Fig. 90b, c), posterolaterally in *sonorensis*, some *tsil*, and most *yuma*; mesopleuron punctate (punctures evanescent in some *yolo*) 32

– Different combination of characters: sternum I apicomesally at most with shallow, ill-defined depression; midscutal setae oriented longitudinally to transversely; mesopleuron punctate or impunctate 40

32. Clypeal lip triangular (Fig. 93b, 97b, 101c), free margin not angulate between lip and lateral section; mandibular inner margin not dentate 33

– Clypeal lip arcuate, concave, or tridentate, free margin angulate between lip and lateral section; mandibular inner margin with tooth (except not dentate in *yolo*) 35

33. Length of flagellomere III about 0.75 of IV (Fig. 101e);

sternal pubescence not velvety; forebasitarsus with preapical rake spines .... *sonorensis* (Cameron), p. 133
– Length of flagellomere III 0.9–1.0 of IV; sternal pubescence velvety (thin in *lamellatus*); foretarsus without rake 34
34. Scutal setae nearly erect, 1.3 MOD long anterolaterally; sternal pubescence not concealing integument; in many specimens hypostomal carina lamelliform and adjacent gena ridged (Fig. 97c) .... *lamellatus* Pulawski, p. 130
– Scutal setae nearly appressed, shorter than MOD anterolaterally; sternal pubescence concealing integument or nearly so; hypostomal carina not lamelliform, gena not ridged .... *huchiti* sp. n., p. 126
35. Sternum I at apex with gradually sloping surface (Fig. 84b); dorsal length of flagellomere I 1.7–2.0× apical width (Fig. 84d); body length 8.5–11.0 mm .... *amplus* W. Fox, p. 115
– Sternum I at apex with horizontal depression; dorsal length of flagellomere I 1.1–1.9× apical width; body length 5–11 mm 36
36. Clypeal lip markedly sinuate (Fig. 99); distance between lip corners about 0.6 of distance between corner and orbit .... *tsil* sp. n., p. 131
– Clypeal lip arcuate, concave, or sinuate (Fig. 90e); distance between lip corners more than distance between lip corner and orbit or slightly less 37
37. Sternal pubescence not velvety .... *yolo* Pulawski, p. 117
– Sternal pubescence velvety 38
38. Clypeal lobe broader (Fig. 88c): lip corners markedly closer to orbit than to each other; propodeal side not ridged or not ridged anteriorly but ridged posteriorly (Fig. 88b); length of flagellomere IV 2.0–2.4× width .... *yuma* Pulawski, p. 120
– Clypeal lobe narrower: lip corners about as distant from orbit as from each other; propodeal side uniformly ridged; length of flagellomere IV up to 2.0× width 39
39. Lip corners more prominent (Fig. 95b), lip base slightly concave, therefore bevel semilunate; setae suberect beneath mesopleural scrobe; southwestern United States, Mexico .... *arizonac* Pulawski, p. 129
– Lip corners less prominent (Fig. 90d, e), lip base straight, bevel not semilunate; setae appressed or nearly so beneath mesopleural scrobe; United States to central Mexico, transcontinental .... *texanus* (Cresson), p. 121
40. Setae erect on scape, vertex (Fig. 55b), and scutum; setae 2.2–3.0 MOD long on vertex, 1.5 MOD on scutum anteriorly; vertex width more than twice length; mesopleuron dull, with inconspicuous punctures; forefemoral notch compressed (its glabrous bottom crestlike); southwestern Texas to southern California, Mexico (Jalisco) .... *idiotrichus* Pulawski, p. 85
– Setae appressed on scape, appressed or shorter than MOD on scutum; no longer than 1.5 MOD on vertex (up to 2.0 MOD long on vertex and scutum in some *psammobius* in which mesopleuron is glossy, coarsely punctate); vertex width in most specimens less than twice length; forefemoral notch not compressed 41
41. Setae of sterna VI–VIII erect, about 1.0 MOD long (Fig. 35a, b); setae of gonoforceps and volsella woolly (Fig. 35c, d); hypoepimeral setae appressed (Fig. 34b); transcontinental except Florida .... *tarsatus* (Say), p. 57
– Sternal setae appressed or (*williamsi*) setae of sterna VI and VIII erect, about 0.4 MOD long; setae of gonoforceps and volsella straight; setae of hypoepimeral area in most species inclined to erect 42
42. Metapleuron with oblique carina or lamella emerging from anterior end of flange; flange broadened (Fig. 103d); tergum I and II unsculptured apically (Fig. 103e); setae of midfemoral venter erect, sparse; malar space present (Fig. 103b) 43
– Metapleuron without carina or lamella below flange; flange narrow or if broadened (many *crassiformis*) than tergum I and II sculptured from base to apex; setae of midfemoral venter appressed to erect; malar space absent 44
43. Metapleuron with single carina that starts beneath anterior end of flange and ends before propodeal spiracle; propodeal side not ridged; setae of propodeal dorsum inclined posterad basally on broad zone that extends from spiracle to spiracle; hindcoxa not carinate; flagellomere III almost as long as IV; forewing with weak, transverse fascia .... *psilocerus* Kohl, p. 139
– Metapleuron with oblique lamella emerging from anterior end of flange (Fig. 103c, d), and with one or two longitudinal carinae behind lamella; propodeal side ridged; setae of propodeal dorsum inclined anterad from base to apex except a few basomedian setae that are inclined posterad; hindcoxa carinate; length of flagellomere III about 0.75 of IV; forewing uniformly colored .... *scopaeus* sp. n., p. 137
44. Tergum I and II unsculptured and glabrous apicomesally (see Fig. 103e); mesopleuron with well-defined punctures; setae of midfemoral venter erect, about 1.0 MOD long .... *papago* Pulawski, p. 137
– Tergum I and II sculptured and setose from base to hindmargin; mesopleuron punctate to impunctate; setae of midfemoral venter appressed to (many *psammobius*) erect, dense 45
45. Clypeal lip sharply pointed to obtusely triangular; mandibular inner margin not dentate or with vestigial tooth (Fig. 12b, 39c, 41c, 57d, 59c, 69e, 71c, 79c) 46
– Clypeal lip arcuate, sinuate, rounded, truncate, or with concave free margin; mandibular inner margin with tooth except not dentate in *occidentalis*, *sulcatus*, and *tipai* (males of *tipai* run either to 46 or to 53 because of varying clypeus shape) 53
46. Pubescence of sterna III–VI velvety, largely or totally concealing integument except apically (Fig. 59d, e) 47
– Sternal pubescence not velvety, not obscuring integument 48
47. Vertex width 1.3–2.0× length; hypoepimeral setae appressed; pubescence of sternum II velvety .... *musciventris* Pulawski, p. 88
– Vertex width 1.1–1.4× length; hypoepimeral setae nearly erect; pubescence of sternum II not velvety .... *tahoe* sp. n., p. 86
48. Sterna II–VI largely glabrous and sparsely punctate mesally; punctures larger on lateral clypeal section than on adjacent frons .... *mirandus* Pulawski, p. 102
– Sterna densely punctate and setose; punctures of same size on lateral clypeal section and adjacent frons 49
49. Propodeal dorsum irregularly ridged to rugose; meso-

pleuron punctate (punctures ill defined in some specimens); vertex setae erect *psammobius* (Kohl), p. 109

– Propodeal dorsum microareolate; mesopleuron at most with inconspicuous punctures; vertex setae appressed to erect 50

50. Length of flagellomere II 2.25–2.5× width; median setae of propodeal dorsum oriented anterad or (some specimens) a few basomedian setae oriented posterad; punctures of mesothoracic venter many diameters apart on each side of midline to (some specimens) no more than one diameter apart; vertex setae erect *tipai* sp. n., p. 99

– Length of flagellomere II 1.6–2.2× width; basomedian setae of propodeal dorsum oriented posterad on about 0.25 of its length; punctures of mesothoracic venter no more than one diameter apart; vertex setae appressed to (some *crenulatus*) erect 51

51. Clypeal lip obtusely triangular to markedly sinuate (Fig. 12b); length of flagellomere II 2.0–2.2× width *angelicus* sp. n., p. 33

– Clypeal lip pointed (Fig. 39c, 41c); length of flagellomere II 1.6–1.8× width 52

52. Punctures of mid- and hindtrochanteral venter several diameters apart to (some specimens) nearly contiguous; corners of clypeal lip closer to each other than to orbits (Fig. 41c); frontal vestiture silvery *crenulatus* W. Fox, p. 65

– Trochanteral punctures nearly contiguous; corners of clypeal lip closer to orbits than to each other (Fig. 39b) in most specimens; frontal vestiture golden in most if not all specimens *spatulifer* Pulawski, p. 63

53. Forefemur not emarginate; mandibular inner margin roundly emarginate (Fig. 50c, d); eastern Cuba, Hispaniola *dominicanus* sp. n., p. 79

– Forefemur emarginate basally; mandibular inner margin not emarginate (except in *cubanus*) 54

54. Vertex longer than wide (width : length ratio = 0.7–0.9); midscutal setae oriented posterad; clypeal free margin markedly concave between lobe and orbit (Fig. 73d); sterna III–VI with well-defined graduli (graduli visible only when sterna are fully extended) 55

– Vertex wider than long; if as wide as long (some *opata*) then midscutal setae oriented radially or transversely, or (some *solaris*) clypeal free margin shallowly concave between lobe and orbit; well-defined graduli present in *glabrior* and *irregularis* 56

55. Clypeal bevel absent or dull, indistinct (Fig. 73d); mesopleuron and propodeal side uniformly microareolate; hindcoxa markedly expanded basodorsally; western United States, northern Mexico (including Baja California) *verticalis* Pulawski, p. 104

– Clypeal bevel well defined, shiny (Fig. 135b); mesopleuron and propodeal side punctate; hindcoxa barely expanded basodorsally; southern half of Mexico, Costa Rica *maya* sp. n., p. 186

56. Mesopleuron with well-defined punctures; propodeal side ridged; gaster black; foretarsal rake absent; and also with characters given under couplet 57 below 57

– Mesopleuron impunctate, with ill-defined punctures, or punctatorugose to rugose; if with well-defined punctures (some specimens), then propodeal side not ridged, or not agreeing with characters given under couplet 57 below 58

57. Clypeal lip (Fig. 77b): distance between corners equal to distance between corner and orbit or slightly less; vertex setae 1.5 MOD long; punctures coarser on mesopleuron than on mesothoracic venter; graduli absent *hurdi* R. Bohart, p. 108

– Clypeal lip (Fig. 81b): distance between corners about 1.25 of distance between corner and orbit; vertex setae 0.3–0.6 MOD long; punctures as fine on mesopleuron as on mesothoracic venter; sterna III–V with graduli *glabrior* Williams, p. 109

58. Midscutal setae oriented radially, forming a rosettelike pattern (as in *ashmeadii*, Fig. 105d, e), but in some individuals midline setae oriented contrastingly posterad (as in *texanus*, Fig. 90b, c); distance between clypeal lobe corners 1.2× clypeal midline (Fig. 75d); axilla the usual shape; mesopleuron finely, evenly punctate; propodeal side not ridged, glabrous along metapleuron *opata* sp. n., p. 106

– Midscutal setae oriented longitudinally or transversely, but if radially (some *crassiformis*, some *pinal*) then distance between clypeal lip corners 1.5–1.8× clypeal midline and axilla expanded in *crassiformis*; mesopleuron and/or propodeal side differently sculptured or propodeal side setose throughout 59

59. Mesopleuron punctatorugose to rugose, punctate beneath; hindcoxa carinate basally; sternal punctures conspicuous, about as large as those on mesothoracic venter; sterna III–VI with well-developed graduli *irregularis* Pulawski, p. 55

– Mesopleuron microareolate, at most with inconspicuous punctures, weakly rugose in some *powelli* in which hindcoxa is not carinate; sternal punctures of most species smaller than those of mesothoracic venter; graduli absent or inconspicuous 60

60. Humeral plate of forewing yellowish or (some individuals) with small, dark spot, contrasting with dark median plate; clypeal free margin not angulate or indistinctly angulate between lip and lateral section (Fig. 63b); most setae of propodeal dorsum oriented transversely *solaris* Pulawski, p. 93

– Humeral plate of forewing dark brown to black or (some species) yellowish anteriorly, not contrasting with median plate; clypeal free margin (except in *occidentalis* and *tipai*) angulate between lip and lateral section; setae of propodeal dorsum oriented anterad or anterolaterad 61

61. Clypeal free margin not angulate or scarcely angulate between lip and lateral section (Fig. 61b, 67e, 69e), lobe ill defined laterally; mandibular inner margin not dentate or with vestigial tooth 62

– Clypeal free margin angulate between lip and lateral section, lobe well defined laterally; mandibular inner margin with tooth 64

62. Clypeal lobe narrow, distance between lip corners about 0.6–0.8 distance between corner and orbit (Fig. 61b); sternal punctures as large as those on mesothoracic venter or larger; apical depression of sterna II–V impunctate (Fig. 61c) *occidentalis* Pulawski, p. 91

– Clypeal lobe broader, distance between lip corners 0.9–

1.0 distance between lip corner and orbit; sterna punctate throughout, punctures finer than on mesothoracic venter 63

63. Vertex width 1.4–1.6× length, vertex setae erect; length of flagellomere II 2.25–2.5× width; mesopleural setae suberect to subappressed below scrobe; punctures of mesothoracic venter less than one diameter to many diameters apart on each side of midline .... *tipai* sp. n., p. 99
– Vertex width 1.1× length, vertex setae nearly appressed; length of flagellomere II 2.0× width; mesopleural setae appressed beneath scrobe; punctures of mesothoracic venter less than one diameter apart .... *sulcatus* sp. n., p. 97
64. Vertex width 2.1–2.3× length (Fig. 27c); corners of clypeal lip (Fig. 27b) about as far from each other as from orbit (ratio: 0.9–1.0); mesopleural setae markedly inclined beneath scrobe; terga I–IV fasciate apically; body length 6–10 mm; Michigan, New Jersey *pechumani* Krombein, p. 50
– Vertex width less than twice length; if 2.0–2.1× length (some *antennatus*, some *krombeini*), then corners of clypeal lip markedly closer to orbits than to each other (ratio: 1.5–1.6), or (some *powelli*) mesopleural setae erect or nearly so beneath scrobe and terga not fasciate 65
65. Corners of clypeal lip (Fig. 6d, 8e, 23, 25f, 29f) closer to each other than to orbit (as 0.45–0.8:1), but equidistant in some *aethiops* (ratio 0.8–1:1); in latter species clypeal lobe delimited laterally by well-defined carina that extends dorsad slightly beyond lip base (Fig. 8f) 66
– Corners of clypeal lip closer to orbit than to each other (as 1.2–1.4:1), but as 0.9–1.3:1 in *pompiliformis*; in latter species clypeal lobe delimited laterally by evanescent carina that does not extend dorsad beyond lip base (Fig. 4c) 70
66. Tergal punctures uniformly, excessively dense (Fig. 30a, b), averaging less than one diameter apart (best visible on apical terga); sterna II–IV impunctate and glabrous apicomesally (Fig. 30c); mountains of northern and central California and adjacent regions of Nevada and Oregon .... *bohartorum* Pulawski, p. 51
– Terga less densely punctate and/or sterna punctate and setose from base to apex 67
67. Clypeal lip: distance between corners equal to 0.6–0.7 of clypeal length (Fig. 23, 25f); gaster all or partly red 68
– Clypeal lip: distance between corners about 0.9 of clypeal length in most specimens (Fig. 6d, 8e), but 0.8–1.0 in *aethiops* (in which gaster is all black in most specimens) 69
68. Sternal punctures finer than those on mesothoracic venter, extending from sternal base to apex; trochanteral venter of many specimens sparsely punctate *eldoradensis* Rohwer, p. 46
– Sternal punctures about as coarse as those on mesothoracic venter; sterna II–IV of most specimens with narrow, impunctate zone apicomesally; trochanteral punctures almost contiguous .... *hopi* sp. n., p. 47
69. Gaster all black to all red; midfemoral venter of many specimens sparsely punctate *aethiops* (Cresson), p. 26
– Gaster red basally; midfemoral venter densely punctate *montanus* (Cresson), p. 25
70. Axilla expanded laterally into lobe that overhangs lateral fossa (Fig. 48d, e); posterior corner of scutum prominent (Fig. 48b) .... *crassiformis* Viereck, p. 75
– Axilla not expanded, not overhanging lateral fossa; posterior corner of scutum rounded 71
71. Setae of sternum VII and VIII inclined to erect, up to 0.4 MOD long (Fig. 37); hypoepimeral setae appressed (see Fig. 34b); West Coast to 100th meridian *williamsi* R. Bohart, p. 62
– Sternal setae appressed; hypoepimeral setae appressed to erect 72
72. Mesopleuron and propodeum (including hindface) uniformly microareolate; hypoepimeral setae appressed; east of 100th meridian, north to North Carolina and Kansas *laevifrons* (F. Smith), p. 56
– Thoracic sculpture different, propodeal hindface ridged in most specimens (not ridged in *toltec*); hypoepimeral setae appressed (many *antennatus*) to erect 73
73. Mesopleuron angulate or weakly carinate between dorsal end of postspiracular carina and anterior end of subalar carina (Fig. 14b); basal half of sternum I with longitudinal, broad keel (Fig. 14c); east of 100th meridian *acutus* Patton, p. 34
– Mesopleuron not angulate or carinate between postspiracular carina and subalar carina; sternum I at most with longitudinal carina 74
74. Apical flagellomeres shorter, maximum length of flagellomere VIII about 1.1× maximum width (Fig. 54c); forefemoral notch with conspicuous pruinosity (Fig. 54d, e); central Mexico *toltec* sp. n., p. 83
– Flagellomeres longer, maximum length of flagellomere VIII no less than 1.5× maximum width; forefemoral notch glabrous or with usual, inconspicuous pruinosity 75
75. Mandibular inner margin roundly emarginate (see Fig. 50c, d); Cuba, Jamaica *cubanus* Pulawski, p. 77
– Mandibular inner margin not emarginate; continental North America 76
76. Setae of propodeal dorsum erect or nearly so in lateral view, about 1.0 MOD long; mesopleuron evenly microareolate (Fig. 19b) *semirufus* (Cresson), p. 40
– Setae of propodeal dorsum erect to markedly inclined anterad in lateral view, no longer than 0.7 MOD; mesopleuron evenly microareolate or differently sculptured 77
77. Mesopleuron with fine microsculpture (Fig. 21c), its punctures minute, about one to many diameters apart; gena thick in dorsal view (Fig. 21e) *pauxillus* W. Fox, p. 42
– Mesopleural microsculpture not conspicuous, punctures larger and/or denser, or mesopleuron impunctate, punctatorugose, or rugose; gena of most specimens thin 78
78. Setae of vertex and mesopleuron erect; forebasitarsus with one to three preapical rake spines that are as long as basitarsal width or longer; terga not fasciate; California and Nevada above 2,700 m .... *powelli* R. Bohart, p. 38
– Setae of vertex and mesopleuron markedly inclined; if vertex setae erect (*pinal*), then forebasitarsus without preapical rake spines; terga I–III of *pinal* fasciate apically 79

79. Vertex setae erect; clypeal lobe (Fig. 52b): distance between corners 1.5–1.6× clypeal length *pinal* sp. n., p. 81
– Vertex setae appressed or nearly so and/or clypeal lobe narrower 80
80. Gaster black; forebasitarsus with three or four preapical rake spines; propodeal side microridged or evenly microareolate; North Carolina to Florida and Alabama *krombeini* Kurczewski, p. 70
– Gaster all or partly red; and/or forebasitarsus with none to two preapical rake spines; and/or propodeal side ridged 81
81. Clypeal lobe broader: distance between corners 1.5–1.6× clypeal length (Fig. 46d); outer apical spine of foretarsomere II shorter than foretarsomere III *antennatus* W. Fox, p. 72
– Clypeal lobe narrower (Fig. 4b): distance between lip corners 0.9–1.3× clypeal length; if ratio is 1.2–1.4 (*miwok*) then outer, apical spine of foretarsomere II as long as foretarsomere III or longer 82
82. Outer apical spine of foretarsomere II as long as foretarsomere III or longer; clypeus (Fig. 43c): distance between lip corners more than distance between corner and orbit; California and adjacent areas of Nevada *miwok* sp. n., p. 67
– Outer apical spine of foretarsomere II shorter than foretarsomere III; clypeus (Fig. 4b): distance between lip corners more to less than distance between corner and orbit 83
83. Gaster apically black, all black in some specimens *pompiliformis* (Panzer), p. 20
– Gaster all red undescribed species, *orestes*, and/or red phase of *pompiliformis*?

Descriptions of the Species

pompiliformis Species Group

The *pompiliformis* group can be defined only by the absence of specializations found in other groups.

Propodeal dorsum and hindface forming obtuse angle; sternum I not carinate except in *acutus*; these two characters also found in *brevipennis*, *brullii*, *euxinus*, and *terminatus* groups (dorsum and hindface forming almost a right angle in *albocinctus*, *erythropus*, *isis*, *julliani*, and *schmiedeknechti* groups). Labrum of most species flat, not protruding beyond clypeal free margin or protruding only slightly, but convex and protruding beyond clypeal margin at least in *ashmeadii* and Palearctic *pusulosus* de Beaumont (labrum convex and protruding beyond clypeal margin in *geniculatus*, *panzeri*, and *undatus* groups). In the female, foretarsomere I not expanded (expanded in *albocinctus* group). In the male, forefemoral notch present except in *dominicanus* and some *psilocerus* (notch absent in *geniculatus* group, and in some species of other groups). Male sterna lack fimbriae and evenly setose in most species, but sterna II–VI largely glabrous mesally in *mirandus* (male sterna fimbriate in *erythropus* and *euxinus* groups, and all or largely glabrous in *albocinctus*, *isis*, *julliani*, and *schmiedeknechti* groups). Prey consists mainly of nymphal acridids, but *fulvitarsis* A. Costa (Palearctic), *semirufus*, and *tipai* provision nests with nyphal tettigoniids. Members of *pompiliformis* group occur in all zoogeographic regions, but in South America only in the Andes.

Systematics.—The laterally oriented midscutal setae combined with the apically depressed sternum I and a punctate mesopleuron are shared by *arizonac*, *huchiti*, *lamellatus*, *sonorensis*, *texanus*, *tsil*, *yolo*, and *yuma*; also *amplus* is similar in spite of its unique sternum I. At least the setal pattern and the shape of sternum I are derived characters, indicating that the species listed above are a closely related lineage within the *pompiliformis* group.

Tachysphex papago is closely related to *psilocerus* and *scopaeus*, as evidenced by two synapotypies: presence of a malar space and peculiar tergal sculpture.

Tachysphex pompiliformis (Panzer)

(Figures 4, 5)

Larra pompiliformis Panzer, 1805:Heft 89, plate 13, ♀. ! Holotype: ♀, Germany: no specific locality (Zool. Samml. Bayer. Staates, Munich, Germany).—In *Tachytes* Shuckard 1837:252.—In *Tachysphex*: Kohl 1885:388 (as synonym of *Tachysphex pectinipes* of Kohl); Richards 1935:163; Pulawski 1971:62 (descr.).

Tachytes nigripennis Spinola, 1808:260, ♀. Holotype or syntypes: ♀, Italy: "prope Genuam" (?lost).—In *Tachysphex*: Kohl 1885:389. Synonymized with *pompiliformis* by Pulawski 1971:62

Larra dimidiata Panzer, 1809:pl. 13, ♀. Holotype or syntypes: ♀, Germany: no specific locality (Zool. Samml. Bayer. Staates, Munich, Germany). Synonymized with *pectinipes* of Kohl by Kohl 1885:388. ! Holotype: ♀, Germany: no specific locality (Zool. Samml. Bayer. Staates, Munich, Germany). Synonymized with *pectinipes* of Kohl by Kohl 1885:388

As *Sphex pectinipes* Linnaeus, 1758 (which actually is a pompilid).—In *Larra*: Dahlbom 1832:53.—In *Tachytes*: Dahlbom 1849:249.—In *Tachysphex*: Kohl 1885:388, de Beaumont 1936:202

Larrada parvula Cresson, 1865:465, ♂. ! Lectotype: ♂, Colorado: no specific locality (ANSP), designated by Cresson 1916:96. **New synonym.**—As synonym of *Larra montana*: Patton 1880:389, Kohl 1885:246.—In *Tachysphex*: W. Fox 1894*a*: 518, Dalla Torre 1897:683, Ashmead 1899:250, Rohwer 1908:223; G. Bohart 1951:951, Krombein 1967:393, Alcock 1973:329; Bohart and Menke 1976:275; Krombein 1979:1929

Larra Quebecensis Provancher, 1882:50, ♀, ♂, incorrect original spelling. ! Lectotype: ♀, Canada: Quebec: no specific locality (Laval Univ. Quebec), **present designation. New synonym.**—Provancher 1883:633 (as sp. n.); Peckham and Peckham 1905:263, Bridwell 1899:208.—In *Tachysphex*: W. Fox 1894*a*:257; Dalla Torre 1897:685; Ashmead 1899:250; J. Smith 1900:518; Harrington 1902: 221, J. Smith 1910:683, Williams 1914:173, Rohwer 1916:687; Gahan and Rohwer 1917:433, G. Bohart 1951:952, Krombein 1967:393; Elliott and Kurczewski 1973:80, Steiner 1973:24; Bohart and Menke 1976:276; Krombein 1979:1629, Finnamore 1982:103

Larra abdominalis Provancher 1887:266

Tachysphex austriacus Kohl, 1892:215, ♀. ! Holotype: ♀, Austria: Vienna area (Naturhist. Mus. Vienna, Austria). Synonymized with *pompiliformis* by Pulawski 1971:62

Tachysphex decorus W. Fox, 1894*a*:524, ♀. ! Holotype: ♀, Dakota: no specific locality (ANSP). **New synonym.**—Dalla Torre 1897:679; Ashmead 1899:250; Cresson 1928:44; G. Bohart 1951:951; Bohart and Menke 1976:275; Krombein 1979:1628

Tachysphex tenuipunctus W. Fox, 1894*a*:525, ♀. ! Lectotype: ♀, Oregon: Mt. Hood (ANSP), designated by Cresson 1928:46. **New synonym.**—Dalla Torre 1897: 686; J. Smith 1910:683; Stevens 1917:422, Mickel 1918:423; Strickland 1947: 129, G. Bohart 1951:953, Newton 1956:615; Ferguson 1962:81; Krombein 1967:393, Bohart and Menke 1976:277, Krombein 1979:1630.

Tachysphex consimilis W. Fox, 1894*a*:526, ♀, ♂. ! Lectotype: ♀, Montana: no specific locality (ANSP), designated by Cresson 1928:44. Synonymized with *parvulus* by R. Bohart *in* Bohart and Menke 1976:275.—Dalla Torre 1897:678; Ashmead 1899:250, H. Smith 1908:382; Williams 1914:164 (as *consimilis* Cresson); Mickel 1918:423, G. Bohart 1951:950.

Tachysphex rufo-niger Bingham, 1897:195, ♀ (incorrect original spelling). ! Lectotype: ♀, "North-West Provinces" [of India or Pakistan?]: no specific locality (BMNH), designated by Pulawski 1975:310. Synonymized by Pulawski 1975: 310

Tachysphex projectus Nurse, 1903:517, ♀. ! Holotype: ♀, Kashmir: no specific locality (BMNH). Synonymized by Pulawski 1975:310.
Tachysphex argyrotrichus Rohwer, 1911:572, ♂. ! Holotype: ♂, Colorado: Las Animas Co.: Trinidad (USNM). Synonymized with *parvulus* by R. Bohart *in* Bohart and Menke 1976:275.—G. Bohart 1951:950.
Tachysphex granulosus Mickel, 1916:413, ♀. ! Holotype: ♀, Nebraska: Sioux Co.: Glen (UNL). Synonymized with *tenuipunctus* by G. Bohart 1951:953.—Mickel 1918:422; Strickland 1947:129.
Tachysphex erythraeus Mickel, 1916:415, ♀. ! Holotype: ♀, Nebraska: Warbonnet Canyon (UNL). **New synonym.**—Mickel 1918:424; G. Bohart 1951:951; Bohart and Menke 1976:273; Krombein 1979:1628.
Tachysphex angularis Mickel, 1916:416, ♂. ! Holotype: ♂, Nebraska: Sioux Co.: Sowbelly Canyon (UNL). **New synonym.**—Mickel 1918:424; G. Bohart 1951: 950; Bohart and Menke 1976:272; Krombein 1979:1627.
Tachysphex unidentified species: Steiner 1981:333.

Diagnosis.—*Tachysphex pompiliformis* is a widespread, common species, but it is difficult to characterize because of considerable variability and lack of a single prominent diagnostic feature. It can be recognized primarily by the microsculptured mesopleuron with shallow, inconspicuous punctures and erect or suberect setae; the finely, densely punctate mesothoracic and trochanteral venter and forefemur; and weak or absent fascia on gastral tergum I. The gaster is bicolored (red basally, black apically) or (some specimens) all black. In the female, the clypeal lip is arcuate, with a lateral incision on each side, and the vertex is wider than long. In the male, the distance between clypeal lobe corners is about equal to the distance between a corner and the orbit, and the foretarsal rake is absent.

Tachysphex pompiliformis is similar to *montanus* and *powelli* (see these species).

Description.—Punctures shallow, subcontiguous on frons; less than one diameter apart on vertex and scutum (but some punctures slightly more than one diameter apart). Mesopleuron dull, microreticulate, with shallow, minute, inconspicuous punctures; hypoepimeral area of some specimens weakly rugose. Propodeal dorsum and side mostly microreticulate, but ridged or rugose in some specimens (especially large ones), and intermediate occur; hindface ridged, but ridges evanescent in small individuals. Sternum I without apical depression. Hindcoxa not carinate.

Setae appressed on scutum and midfemoral venter.

Head, thorax, and legs black, tarsal apex brown or reddish. Gaster all black in some individuals, but two or three basal segments red in most specimens. Tergal fasciae varying. Wings infumate, but only weakly so in the smallest males.

♀.—Clypeus (Fig. 4a): bevel shorter to longer than basomedian area; lip arcuate, without mesal notch, incised laterally. Dorsal length of flagellomere I 1.8–2.3× apical width. Vertex wider than long. Discal micropuntures of tergum II two to several diameters apart. Tergum V densely punctate, but apical depression often impunctate. Pygidial plate alutaceous, sparsely punctate. Trochanteral and femoral punctures fine, dense. Length 7–11 mm.

Frontal vestiture not totally obscuring integument between antennal socket and orbit (except in occasional individuals). Vertex setae subappressed to suberect, about 0.7 MOD long.

Frontal vestiture silvery or with golden tinge.

♂.—Mandibular inner margin with tooth (Fig. 4b). Clypeus (Fig. 4b, c): bevel as long as basomedian area or much shorter; lip arcuate or sinuate, distance between corners equal to 0.9–1.3 of clypeal length and also of distance between corner and orbit. Dorsal length of flagellomere I 1.2–1.6× apical width. Vertex width 1.4–1.7× length. Sterna densely punctate and pubescent throughout. Forefemoral notch glabrous. Foretarsus in most specimens without rake; outer apical spine of tarsomere II shorter than foretarsomere III. Length 5–8 mm.

Integument totally obscured by vestiture between antennal socket and orbit as seen from certain angles. Vertex setae subappressed to erect, 1.0 MOD long. Frontal vestiture silvery to brassy golden.

Variation.—Northern specimens (Yukon Territory, Northwest Territories) average larger than southern individuals.

In most females the integument is not totally obscured by vestiture between orbit and antennal socket, but it is totally hidden in three females from Stockton, Manitoba (CNC).

In most females terga I–III are silvery fasciate apically (fascia of tergum I inconspicuous), but tergum IV is also fasciate in two females from Saskatchewan: Attons Lake and Saskatoon (CNC). Only tergum II is fasciate or all fasciae are evanescent in many females from Alberta, British Columbia, Washington, Oregon, and California.

Most males have pale golden frontal vestiture, and nonfasciate tergum IV, but in most males from eastern Canada (Nova Scotia, Prince Edward Island, Quebec), the frontal vestiture is silvery or with golden tinge, and terga I–IV are fasciate apically. In many males from western Canada (Alberta, British Columbia), the frontal vestiture is brassy golden, and apical fasciae are present on terga I–III (fascia of tergum I evanescent in most specimens).

The forebasitarsus of most males has only the apical spine on outer margin, but a preapical spine is present in a male from Stockton, Manitoba (CNC) and a male from Elbow, Saskatchewan (CNC); two short, preapical spines are present in one of the six males examined from Bear Creek, Idaho (UIM).

The lip corners of the male clypeus are closer to the orbits than to one another in most specimens, but they are equidistant in some individuals from Alberta and slightly closer to each other than to orbits in a male from Squamish, British Columbia (CNC).

The first two or three gastral segments are red in most specimens, but only tergum II is red in some individuals. Also segment IV is red in a female from Buckeye Reservoir, Colorado (CSU). Occasionally the gaster is all black, especially in specimens from higher altitudes and latitudes, or has a reddish preapical shadow on terga I and II.

Discussion.—*Tachysphex pompiliformis* is a Holarctic species, a fact unrecognized in both the Palearctic and Nearctic regions. Nearctic populations have been treated under several names (see synonymy), of which *parvulus* and *tenuipunctus* were the most commonly used. There are slight differences between Old and New World *pompiliformis*. The propodeal side is ridged in most Palearctic specimens, but evenly microsculptured in some, e.g., from Leningrad area, as it is in most North American specimens.

Tachysphex pompiliformis is difficult to define, and several undetermined phena may actually belong to this species. Another possibility is that I have assigned a cluster of similar, unrecognized species to *pompiliformis*. In particular, I do not know whether *pompiliformis* may have an all red gaster (many such specimens look like *pompiliformis*, but possibly they are another species).

Note on *Tachysphex quebecensis*.—Provancher called this

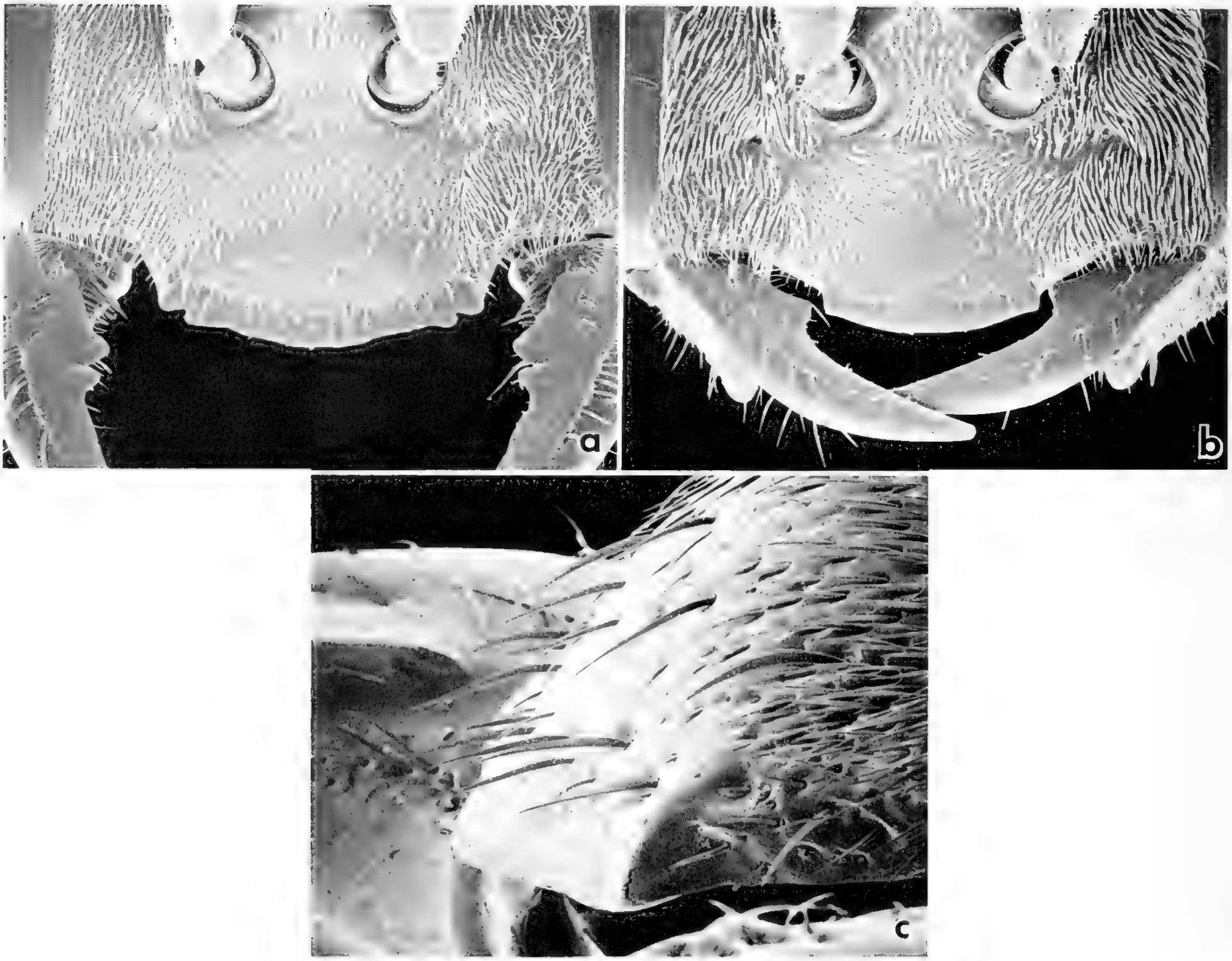

FIGURE 4 *Tachysphex pompiliformis* (Panzer): a—female clypeus; b—male clypeus; c—male clypeus obliquely from the side.

species *Larra quebecensis* in 1882 and 1883, but referred to it as *Larra abdominalis* in 1887. Gahan and Rohwer (1917–18) were unable to locate the syntypes of the former name in Provancher's collection, but individuals labeled as *Larra abdominalis* are present there. I have accepted these as the type material of *quebecensis*.

The type of *quebecensis* and several other specimens examined have the propodeal dorsum and side ridged and rugose. In most *pompiliformis* these parts are uniformly microareolate, but the two extremes are connected by a range of intermediates; e.g., the dorsum is microrugose or irregularly ridged basally, and the side is microreticulate or finely ridged. The complete range of intermediates from ridged to nonridged propodeum can be found within a single population, e.g., in specimens from Alger County, Michigan (UMMZ), or Huron Mountain Club, Michigan (CAS, UMMZ).

LIFE HISTORY.—Observations of European writers were summarized by Pulawski (1971). In Europe, *pompiliformis* nests in flat or sloping areas, sometimes in cliffs. Nest construction precedes provisioning. There are one to three cells per nest, but one is usual. The nest entrance is permanently open during the provisioning period. The prey consists of acridid nymphs, which are flown to the nest or transported on the ground. During transport the wasp straddles the acridid, which is oriented dorsum up and held by the antennae with the wasp's mandibles. One to ten prey are deposited in a cell, depending on their size. The egg is laid on the largest prey at the end of the provisioning.

In North America the life history of *pompiliformis* was observed by Peckham and Peckham (1905, as *quebecensis*) in Wisconsin, by Newton (1956, as *tenuipunctus*) near Shoshone, Idaho, and by Alcock (1973, as *parvulus*) near Seattle, Washington. These observations are incomplete, but they agree with European reports. All nests were in flat areas; they were unicellular and open during the provisioning period. The nests examined by Alcock (1973) were oblique to the surface (5.5 cm long, ending 2.5–3.5 cm below the soil surface). Prey carriage is the same as in European specimens, although Peckham and Peckham (1905) state that the wasp holds the prey "in her third legs." The Peckhams observed that the wasp deposits prey at the nest entrance first and then drags it backwards inside the

nest. At Shoshone two small prey per cell were deposited in early June, but only one large prey in late June; the nest observed by the Peckhams was provisioned with three prey. Most prey collected near Shoshone were *Oedaleonotus enigma* (Scudder), but a few *Aulocara elliotti* (Thomas) and one *Melanoplus* sp. were also observed. Krombein (1967, as *quebecensis*) lists immature Acrididae (*Camnula, Melanoplus*). A female examined from Dickinson, North Dakota (USNM) is pinned with her prey, a nymph of *Melanoplus* sp., and a female from Mt. Rose, Nevada (UCD) with an acridid nymph, probably *Aulocara* (det. D. C. F. Rentz). The sarcophagid fly *Taxigramma heteroneura* (Meigen) is a parasite. Another parasite, the mutillid *Sphaerophthalma orestes* (Fox), was reported by Ferguson (1962) from Merrill, Oregon. Flower records: males from Cottonwood, Idaho, were collected on *Eriogonum*, and males from Sand Dune Lake, Idaho, on *Helianthus* (UIM). There is one generation per year at Shoshone.

Steiner (1981) found that the prey of this species is paralyzed with four consecutive stings and described the stinging sites on the prey's body.

Geographic Distribution (Fig. 5).—*Tachysphex pompiliformis* is now known to be Holarctic. In North America it is transcontinental but largely northern. It ranges north to Prince Edward Island and the delta of the Mackenzie River, south to New York and Michigan. In the west, it occurs in mountains of Colorado and the Sierra Nevada in California.

In the Old World the species is widespread. It occurs from the eastern coast of Ireland to Kamchatka. It ranges northward to Scotland (except Highlands), to the polar circle in Finland (Rovaniemi), and to Yakutsk in Siberia. Its southern limits include the northern Mediterranean countries, Morocco, Turkey, northern Iran (Elburz Mountains, Meshed), Kashmir, and Ulan Baator in Mongolia. *Tachysphex pompiliformis* is apparently absent from the Transcaspian deserts.

Material Examined.—1,043♀, 919♂.

Records.—CANADA: **Alberta:** Banff, Beaver Lodge, Beverly, Brooks, Cowley, Drumheller, Elkwater Park, Empress, Frank, Jumping Pd. Creek (20 mi W Calgary), Laggan (=Lake Louise), Lethbridge, McMurray, Medicine Hat (also 25 mi NW), 15 mi E Morley, 12 km SW Orion, Raymond, Red Deer, Scandia, Taber, Turin, Wainwright, Waterton Park, Writing-on-Stone Provincial Park. **British Columbia:** Agassiz, Carbonate Columbia River, Chapmans (Frazer River), Galiano, Hatzic Lake, Kaslo, 20 mi S Lytton (Frazer River), Merritt, Minnie Lake, Mission City, North Thormanby Island, Okanagan, Orofino Mt. near Oliver, Racing River, Revelle Lake, Robson, Squamish, Taylor, Yale Region (4 mi W Princeton). **Manitoba:** Aweme, Bird's Hill Province Park (15 mi N Winnipeg), Boisevain, 6 mi NW Brandon, Churchill, Emerson, Falcon Lake (15 mi E Rennie), Horton, Melita, mile 503 Hudson Bay Highway, 30 mi N Roblin, 5 mi SW Shilo, Spruce Woods Province Park (8 mi N Glenboro), Stockton, Whitewater. **New Brunswick:** Nerepis, Peticodiac. **Northwest Territories:** Aklavik, Fort Providence, Mackenzie Delta, Normal Wells, Rae, Yellowknife. **Nova Scotia:** Baddeck, Cape Breton Island, Hants Cove, Kentville, Lockeport, Sable Island, Truro. **Ontario:** Gravenhurst (Muskoka District), Kearney, Longbow Corners (11 mi E Kenora). **Prince Edward Island:** Brackley Beach, Dalvay House in Prince Edward Island National Park. **Quebec:** Burbidge, Kazabazua, Mont Joli, Old Chelsea, Sainte Anne de la Pocatière, Sully. **Saskatchewan:** Attons Lake W Cut Knife, Big River, Christopher Lake, Elbow, Good Spirit Lake, Moose Jaw, Parkbeg, Pike Lake, Prince Albert, Rutland, Saskatoon, 5 mi E Swift Current, Willoe Bunch. **Yukon Territory:** Minto Landing Territorial Campground (Klondike Loop J-148), Watson Lake, Whitehorse.

UNITED STATES: ALASKA: Matanuska. ARIZONA: **Apache:** Alpine, Greer, McNary. **Cochise:** Ramsey Canyon in Huachuca Mts. **Coconino. Graham:** Hospital Flat (Pinaleno Mts.), Mt. Graham. **Greenlee:** Hannagan Meadows. **Mohave:** Grand Canyon (North Rim). CALIFORNIA: **Alpine:** Carson Pass, Hope Valley, Winnemucca Lake. **Amador:** 4 mi N Silver Lake. **Contra Costa:** Las Trampas Ridge W Danville. **Del Norte:** Beans Camp, Crescent City. **El Dorado. Fresno. Humboldt:** Big Lagoon, Patricks Pt., Red Cap Lake. **Inyo. Lassen:** Bridge Creek Camp. **Madera:** Green Mtn. (S Mariposa on county line). **Marin:** McClure's Beach, Point Reyes, Tomales. **Mariposa:** Yosemite National Park (Crane Flat, Glacier Point, Tenaya Lake). **Mendocino:** 4 mi E Point Arena, Mendocino, Navarro River 3 mi SE Paul M. Dimmick State Park. **Modoc. Mono. Monterey:** Paraiso Springs. **Nevada:** Boca, Sagehen Creek near Hobart Mills, 7 mi SE Truckee. **Placer:** Carnelian Bay on Lake Tahoe, Tahoe. **Plumas. San Bernardino:** San Bernardino Mts. **San Francisco:** San Francisco. **San Mateo:** San Bruno Mts. **Santa Cruz:** Big Basin. **Shasta:** 4 mi S Burney, Lassen Peak, Summit Lake. **Sierra. Siskiyou. Sonoma:** —. **Stanislaus:** Evergreen Road 3.2 mi W Highway 120. **Trinity:** Big Flat (Coffee Creek), Carrville, Scott Mt. **Tulare. Tuolumne. Yolo:** Rumsey. COLORADO: **Alamosa:** Mosca. **Boulder. Chaffee:** Buena Vista, 7,800 ft. **Clear Creek. Costilla:** Russel, Ute Creek. **Custer:** Alvarado Creek (Sangre de Cristo Mts.), Westcliffe. **Delta:** Grand Mesa. **Denver:** Denver. **Douglas:** 20 mi S Denver, Longview. **Eagle:** Tennessee Pass. **El Paso. Gilpin:** Pinecliffe. **Grand:** Granby, Troublesome. **Gunnison:** Lead King Basin. **Jackson. La Plata:** Bayfield. **Larimer. Mesa:** 31 mi N Mack, Pinon Mesa. **Montrose:** Buckeye Reservoir. **Park:** Grant, Jefferson, Wilkerson Pass. **Pitkin:** Ajax Mt. near Aspen. **Rio Grande:** South Fork. **Routt. Teller:** Florissant. **Weld:** 1 mi NE Nunn. IDAHO: **Bear Lake:** 9 mi E Montpellier, 5 mi W Ovid. **Blaine. Boise:** 3 mi NE Garden Valley. **Bonner:** Blanchard. **Boundary:** 2 mi S Naples. **Butte:** Bear Creek Pass, Craters of the Moon National Monument. **Cassia:** Emery Canyon (12 mi SE Oakley). **Clark:** 13 mi NE Kilgore. **Clearwater:** Elk River. **Custer. Franklin:** Cub River Canyon, 8 mi E Mink Creek. **Fremont:** 10 mi NE Ashton, Bootjack Ferry, Box Canyon (Island Peak). **Gem:** Emmett. **Idaho:** 6 mi SE Grangeville, Lolo Pass Shotgun Creek, Warren. **Kootenai:** Lane. **Latah:** Moscow (also 7 mi N, Moscow Mtn. **Lemhi:** 2 mi N Gilmore, Lemhi Pass. **Lincoln:** Dietrich Butte, Shoshone. **Oneida:** Black Pine Canyon, Salyer Cow Camp. **Owyhee:** Walter's Ferry, Sand Dune Lake. **Shoshone:** 4 mi N Avery (also 7 and 10 mi E, 8 mi N), Red Ives Research Station (also 5 mi NW). **Valley:** Darling's Flat (S Fork Salmon River), Lake Fork, 4 mi W McCall. MAINE: **Cumberland:** Portland. **Hancock:** Hancock. **Lincoln:** Waldoboro. **Penobscot:** Orono. **Sagadahoc:** Brunswick. MASSACHUSETTS: **Middlesex:** Reading. MICHIGAN: **Alger:** Pictured Rocks National Lakeshore. **Baraga:** Pequaming. **Benzie:** —. **Charlevoix:** Thumb Lake. **Colfax, Emmet, Gladwin, Grand Traverse, Iosco:** —. **Iron:** Crystal Falls. **Kalkaska, Keweenaw:** —. **Marquette:** Huron Mountain Club, Marquette, Yellow Dog Plains. **Midland:** —. **Muskegon:** Muskegon State Park. **Osceola:** Tustin. **Schoolcraft:** Floodwood. MINNESOTA: **Blue Earth:** Mankato. **Itasca:** Itasca Park. **St. Louis:** Duluth. MONTANA. **Beaverhead:** 3 mi W Jackson. **Dawson:** Glendive. **Gallatin:** Three Forks. **Hill:** Simpson. **Madison:** 16 mi S Cameron, 9 mi N Ennis, Louise Lake. **Meagher:** White Sulphur Springs. **Missoula:** 3 mi S Arlee. **Park:** Gardiner. **Ravalli:** Hamilton, Sula. NEBRASKA: **Douglas:** Omaha. **Hooker:** Dismal River 15 mi S Mullen, 1.5 mi N Mullen. **Sheridan:** Bingham. **Sioux:** Monroe Canyon, Sowbelly Canyon. NEVADA: **Elko. Humboldt:** Winnemucca. **Lander:** 40 mi N Austin, Kingston Recreation Area (Toiyabe Mts.). **Lincoln:** Hiko Range. **Nye:** 10 mi N Gabbs. **Washoe:** Mt. Rose, Steamboat. **White Pine.** NEW HAMPSHIRE: **Coos:** Crawford's. **Grafton:** Franconia, White Mts. NEW MEXICO: **Colfax:** 5 mi S Eagles Nest, Raton, 2 mi W Ute Park. **Otero:** Cloudcroft, Weed. **Sandoval:** Jemez Springs. **San Miguel:** Beulah, Pecos. **Santa Fe:** Little Tesuque Canyon near Santa Fe. **Taos:** Taos. NEW YORK: **Franklin:** —. **Madison:** Chittenango. **Oswego:** Oswego. **Saint Lawrence:** Parishville. **Tompkins:** Freeville, McLean. NORTH DAKOTA: **Bottineau:** Bottineau. **Bowman:** Gascoyne. **Grand Forks:** Northwood. **Hettinger:** Mott. **McHenry:** Towner. **McLean:** Washburn. **Ramsey:** Devils Lake. **Richland:** 12 mi W Walcott. **Stark:** Dickinson. OREGON: **Baker:** Cornucopia. **Benton:** Corvallis, 5 mi W Lewisburg. **Clackamas:** Mt. Hood. **Curry:** Winchuck River (mouth). **Deschutes:** Deschutes River 1 mi SW Pringle Falls. **Harney:** Blitzen River headwaters (Steens Mts.), 4 mi NE Flagstaff Butte. **Hood River:** Mt. Hood. **Klamath. Lane:** Horse Lake (High Cascade Mts.), 10 mi E Oakridge. **Lincoln:** Newport, Yaquima Bay. **Marion:** Silver Creek Peak. **Polk:** Black Rock (10 mi SW Dallas). **Wallowa:** Wallowa Lake. **Washington:** Cornelius, Forest Grove. SOUTH DAKOTA: **Brown:** Hecla. **Custer:** Custer. **Pennington:** Badlands National Park. UTAH: **Box Elder. Cache. Carbon:** Price Canyon Recreation Area (1 mi W Castle Gate). **Daggett:** Ridge Camp (30 mi N Vernal). **Davis:** Bountiful Peak. **Duchesne:** Roosvelt. **Emery:** Huntington Creek, Orange Olsen Ranger Station. **Garfield:** 15–16 mi N Boulder, Boulder Mtn. **Grand:** LaSal Mts., 12 mi N Moab. **Iron:** Cedar Breaks, Deer Valley, Miner's Peak. **Juab:** Mt Nebo. **Kane:** Duck Creek Camp, Navajo Lake. **Millard:** Oak Creek Canyon (Oak City). **Rich:** Bear Lake, Logan Canyon summit, Monte Cristo. **Salt Lake:** Midvale Mill Creek Canyon, Salt Lake City. **Sanpete:** Ephraim, Moroni. **Uintah. Utah:** Lehi, Provo. **Wasatch:** Guardsman Pass near Brighton, Park City. **Washington:** St. George, Upper Deep Creek. **Weber:** Beaver Creek (head), Ogden, Willard Peak. VERMONT: **Rutland:** Chittenden. **Windham:** Jamaica. WASHINGTON: **Clark:** Vancouver. **King:** Seattle. **Kittitas:** Fish Lake. **Klickitat:** Brooks State Park. **Pacific:**

FIGURE 5. Geographic distribution of *Tachysphex pompiliformis* (Panzer) in North America.

Bay Center, Long Beach, Nahcotta, Seaview. **Pend Oreille:** Metaline Falls. **San Juan:** Argyle (San Juan Island), Friday Harbor, Lopez Island. **Thurston:** Olympia. **Walla Walla:** Mill Creek. **Whitman:** Lyle Grove near Pullman, Pullman (Smooth Hill). **Yakima:** Mt. Adams. WISCONSIN: **Clark:** Worden Township. **Oneida:** Woodruff. WYOMING: **Albany:** 10 mi SE Laramie (also 13 mi NE), Summit. **Big Horn:** 10 mi E Shell. **Converse:** Glenrock. **Fremont:** Brooks Lake (Shoshone National Forest), Sweetwater River at Highway 28, Union Pass Road. **Lincoln:** 2 mi S Alpine, Dietrich Butte. **Park:** Lake Creek Camp (13 mi SE Cooke City, Montana). **Platte:** Glendo. **Sheridan:** Bighorn, Long Park (20 mi SW Big Horn). **Sublette:** Green River Lakes, 3 mi N Pinedale. **Sweetwater:** Green River. **Teton** (excluding Grand Teton and Yellowstone National Parks). **Teton** (Grand Teton National Park). **Yellowstone National Park.**

Tachysphex montanus (Cresson)

(Figures 6, 7)

Larrada montana Cresson, 1865:465, ♀. ! Lectotype: ♀, Colorado: no specific locality (ANSP), designated by Cresson 1916:96.—Cresson 1876:208.—In *Larra:* Patton 1881:389; Ashmead 1890:33.—In *Tachysphex:* W. Fox 1894*a*:523; Dalla Torre 1897:681; Ashmead 1899:250; G. Bohart 1951:951; Krombein 1967:393; Bohart and Menke 1976:275; Krombein 1979:1628.

Tachysphex inusitatus W. Fox, 1894*a*:524, ♂. ! Holotype: ♂, Colorado: no specific locality (ANSP). Synonymized by G. Bohart 1951:951.—Dalla Torre 1897:680; Ashmead 1899:250; Cresson 1928:45.

Tachysphex compactus W. Fox, 1894*a*:528, ♂. ! Holotype: ♂, British Columbia: Vancouver (ANSP). Synonymized by G. Bohart 1951:951.—Dalla Torre 1897: 678; Ashmead 1899:250; Harrington 1902:221; Cresson 1928:44.

Tachysphex triquetrus W. Fox, 1894*a*:528, ♀. ! Holotype: ♀, Nevada: no specific locality (ANSP). Synonymized by Pulawski *in* Krombein 1979:1628.—Dalla Torre 1897:686; Ashmead 1899:250 (as *triqutrus*); Cresson 1928:46; G. Bohart 1951:953; Bohart and Menke 1976:277.

Diagnosis.—The female of *montanus* can be recognized by the sculpture of the forefemur: the fine punctures (which are dense or sparse basoventrally) are superimposed basoventrally with large, sparse, punctures (Fig. 6b, c). In other species, the forefemoral venter is evenly micropunctate (large punctures absent or inconspicuous), or (*aethiops*) only large punctures are present, or (*mirandus, tipai*) all punctures are fine, sparse. The forefemoral punctation is similar in *montanus*, many *powelli*, and some *pompiliformis*, but unlike the latter two species, the females of *montanus* and *aethiops* have an unusually deep subalar fossa (the anterior half of its bottom intersects the posterior half at about a right angle). In addition, the gaster of *montanus* is red (at least basally), but is all black in most *powelli*.

The male of *montanus* is very similar to *aethiops*. See that species for differences.

Description.—Frontal punctures nearly contiguous. Vertex punctures subcontiguous to about one diameter apart. Mesopleuron microsculptured, with shallow, inconspicuous punctures. Propodeal dorsum evenly microareolate, also slightly ridged basally in some specimens; side microsculptured or weakly ridged; hindface ridged or ridges evanescent above. Sternum I without apical depression. Discal micropunctures of tergum II one to two diameters apart. Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit. Setae suberect, shorter than MOD on vertex and scutum, but erect, 1.0 MOD long on postocellar impression, appressed on femora.

Head, thorax, and legs black, tarsal apex reddish. Gastral segments I–III red, the remainder black or red. Terga not fasciate. Wings weakly infumate. Frontal vestiture silvery in most specimens, but golden in males from Dry Lake Mountain, California.

♀.—Clypeus (Fig. 6a): bevel equal to basomedian area or longer, in most specimens concave anteriorly (shallowly to deeply); lip arcuate, broadly incised laterally, in most specimens weakly emarginate mesally. Dorsal length of flagellomere I 2.3–2.7× apical width. Vertex wider than long. Scutal punctures fine, on disk averaging one to two diameters apart. Subalar fossa deep, the anterior half of its bottom intersecting the posterior half at about a right angle. Tergum V densely punctate (sometimes sparsely mesally), its apical depression impunctate. Pygidial plate shiny, punctate. Forefemur finely, densely punctate, and also with large, sparse, conspicuous punctures (Fig. 6b, c); see Variation below for details. Length 11–14 mm.

♂.—Mandibular inner margin with tooth (Fig. 6d). Clypeus (Fig. 6d): bevel about as long as basomedian area or shorter; lip arcuate, its corners rectangular, separated by a distance that equals 0.6–0.8 of distance between a corner and orbit and about 0.8–1.0 of clypeal length; sharp carina emerges from lip corners and extends slightly beyond lip base. Dorsal length of flagellomere I 1.6–1.8× apical width. Vertex width about 1.7× length. Sterna densely punctate. Forefemoral notch glabrous. Forebasitarsus with none to two preapical spines; outer apical spine of foretarsomere II shorter than foretarsomere III. Length 8.5–10.0 mm.

Variation.—*Mesopleural setae.* Nearly appressed in most specimens, but nearly erect in individuals from southern California (13 mi E Amboy, Borrego Valley, Glamis, 20 mi E Glamis, Needles), and also in some specimens from Idaho: Lincoln Butte (1♂, UCD), Oakley area (2♂, UIM), Parowan Canyon, Utah (1♂, UCD), and Sunnyside area (1♂, UIM). There is some intergradation in this character.

Trochanteral punctures (female). The trochanteral venter is closely punctate in many specimens, but sparsely punctate in the females in which the forefemoral micropunctures are sparse basoventrally. In addition, the trochanteral venter is sparsely punctate in some females in which the forefemoral micropunctures are uniformly dense, e.g., in individuals from Borrego Valley (1♀, UCD) and Glamis (1♀, UCD).

Forefemoral punctures (female). Micropunctures are uniformly dense in most females, but sparse basoventrally (several to many diameters apart) in some. Full intergradation from one state to another may be observed within the same population (e.g., 6 mi N Cedarville, California). Females with sparse forefemoral micropunctures have been observed in the following localities: California: 6 mi N Cedarville (1♀, UCD), Sagehen Creek (1♀, CAS; 2♀, UCD), Tahoe (1♀, UCD); Oregon: Cornucopia (2♀, CAS, UCD).

Midfemoral punctures. In most individuals, the punctures of midfemoral venter are no more than one diameter apart, but up to several diameters apart in some females from Rainbow Valley, Arizona, and in some males from southern California. Intergradation in this character was observed in the females from Rainbow Valley, and punctation varies from dense to sparse in males collected 18 mi W of Blythe, California.

Discussion.—*Tachysphex montanus* is not easily defined, and many females closely resemble *pompiliformis*, while males are similar to *aethiops*. Furthermore, *montanus* occurs in diverse habitats: from alpine zone (White Mts., California) to lowland sand dunes (Borrego Valley and Glamis, California). In spite of the difficulties of defining it, I regard *montanus* as a good species. The sex association is beyond doubt: both males and females

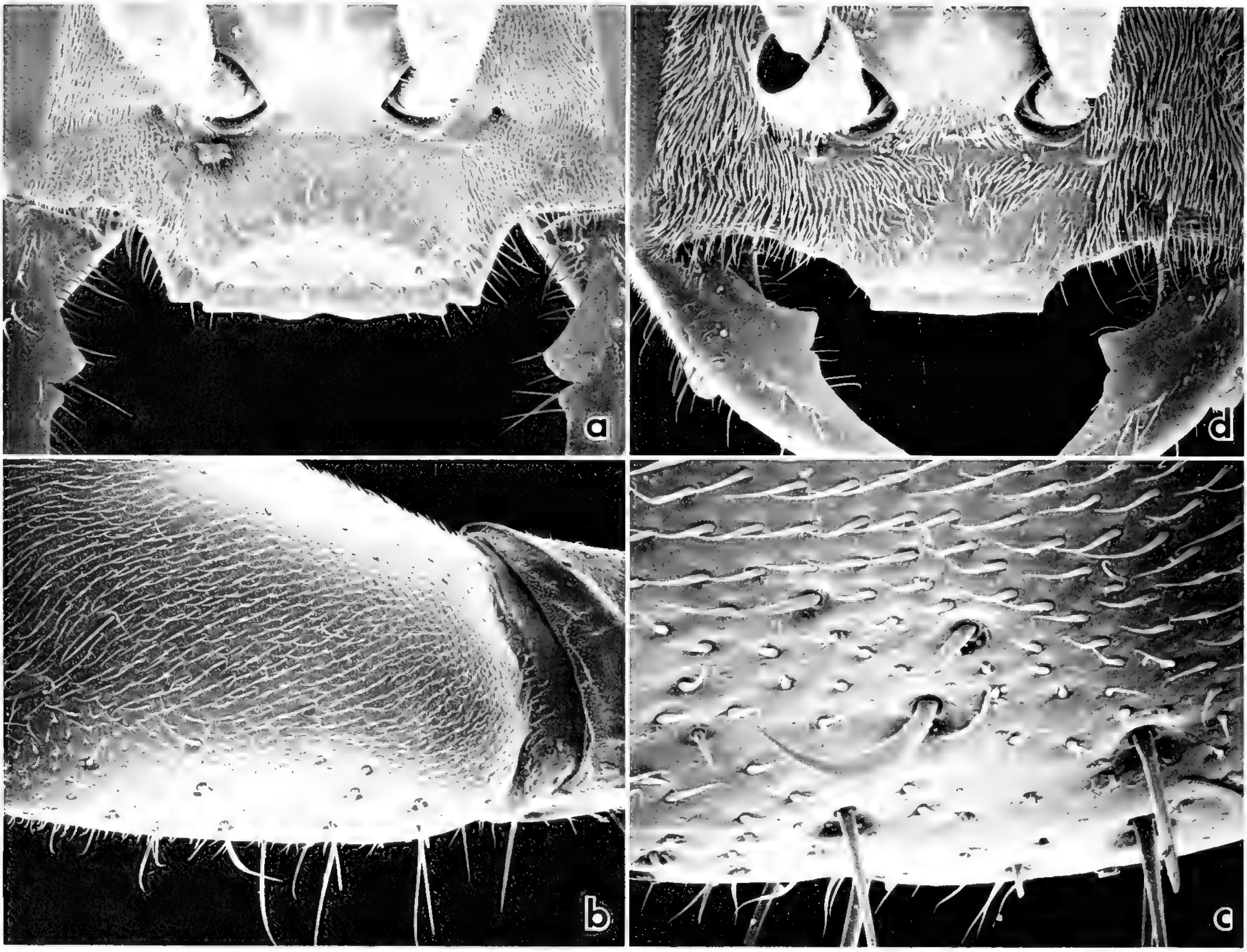

FIGURE 6. *Tachysphex montanus* (Cresson): a—female clypeus; b—forefemoral venter of female; c—same, higher magnification; d—male clypeus.

have been collected together at several localities, e.g., in Borrego Valley, Glamis, and Sagehen Creek, California; and in Cornucopia, Oregon.

The holotype male of *inusitatus* is a deformed specimen with strongly depressed vertex and occiput. Otherwise it agrees with *montanus*.

LIFE HISTORY.—Females of *montanus* prey upon nymphal *Oedaleonotus* (Acrididae) according to Krombein (1967). The specimens to which he refers (USNM) were collected at Owinza, Idaho (Newton 1956). Prey length varies from 8 to 15 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 7).—Southern British Columbia to southern California and Arizona, east to Alberta, Idaho, and Colorado.

MATERIAL EXAMINED.—59♀, 59♂ (ANSP, CAS, CSDA, CU, MCZ, TLG, UCD, UIM, USNM, USU, WJP).

RECORDS (b: individuals with black gastral apex).—CANADA: **Alberta:** Writing-on-Stone Provincial Park (b). **British Columbia:** Vancouver (b).

UNITED STATES: ARIZONA: **Maricopa:** Phoenix, Rainbow Valley. **Yuma:** Parker (b). CALIFORNIA: **Glenn:** Plaskett Meadows. **Humboldt:** 5 mi NW Garberville. **Imperial:** Glamis (also 20 mi E). **Modoc:** 6 mi NW Cedarville. **Mono:** White Mts., elevation 10,000 ft (partly b). **Nevada:** Boca, Sagehen Creek near Hobart Mills. **Placer:** 5 mi NW King's Beach, Tahoe. **Plumas:** Meadow Valley. **Riverside:** 18 and 22 mi W Blythe, Hopkins Well (about 20 mi W Blythe). **San Bernardino:** 13 mi E Amboy, Needles. **San Diego:** Borrego Valley. **Siskiyou:** Dry Lake Mountain (7 mi NNW town of Klamath River), Salmon Mt. COLORADO: **Costilla:** Ute Creek, 9,000 ft (b). IDAHO: **Cassia:** Burley (b), 5 mi S Oakley (b). **Elmore:** 6 mi S Sunnyside (b). **Idaho:** Moose Creek Ranger Station near Grangeville. **Lincoln:** Dietrich Butte (partly b), Owinza (between Dietrich and Kimama), Shoshone (b). **Minidoka:** 9 mi NE Kimama (b). **Shoshone:** Clarckia (Crater Peak). NEVADA: —. OREGON: **Baker:** Cornucopia. **Jackson:** Ashland Mt. UTAH: **Cache:** Logan (b). **Iron:** Parowan Canyon. **Sevier:** Richfield. **Utah:** Provo (b). WYOMING: **County unknown:** Bridger Basin (S Gorman) (b).

Tachysphex aethiops (Cresson)

(Figures 8, 9)

Larrada Aethiops Cresson, 1865:465, ♀ (incorrect original spelling). ! Lectotype: ♀, Colorado: no specific locality (ANSP), designated by Cresson 1916:95.—In *Larra*: Patton 1879:354, 1881:389, Kohl 1885:240, Ashmead 1890:33.—In *Tachysphex*: W. Fox 1894*a*:529, Dalla Torre 1897:677, Ashmead 1899:250; Bridwell 1899:208, Rohwer 1908:223, G. Bohart 1951:950; Krombein 1958*c*:188, Evans 1970:489, 497; Alcock 1973:329, Elliott and Kurczewski 1973:80, Evans 1973:149, Steiner 1973:23, Bohart and Menke 1976:272; Krombein 1979:1627, Finnamore 1982:103.

DIAGNOSIS.—The female of *aethiops* can be recognized easily by the shiny, sparsely punctate fore- and midfemoral venter

(Fig. 8c, d), and the pygidial plate is punctatorugose in most specimens (Fig. 8b). The femoral sculpture is similar in *mirandus* and *tipai*, but in both the vertex setae are 1.0 MOD long (up to 0.6 MOD in *aethiops*), the length of flagellomere II is 3.5–4.0× width (2.8–3.2 in *aethiops*), and the wings are hyaline to moderately infumate (strongly infumate in *aethiops*). In addition, the body length and the vertex width : length ratio are: 11–13 mm and 1.5–1.7 in *aethiops*, 8–12 mm and 1.1–1.6 in *mirandus*, and 6.5–8.0 mm and 1.1–1.3 in *tipai*.

The male of *aethiops* is very similar to *montanus*. The two differ from the other species in having a dull, impunctate mesopleuron, nonfasciate terga, and a distinctive clypeus (Fig. 6d, 8e); the lobe is delimited laterally by a small but sharply defined carina that emerges from the lip corner and extends dorsad slightly beyond the lip base; the distance between the lip corners is equal to 0.8–1.0 of the clypeal length. The clypeal lobe is similar in *bohartorum* (carinate anterolaterally, width : length ratio equal to 0.7–0.8), but the excessively dense tergal punctation of that species (Fig. 30a, b) is distinctive. In other species the clypeal lobe is either narrower (*eldoradensis, hopi*) or markedly broader, or the lateral carina is evanescent to absent. Males of the two species are not easily separated. In most *aethiops* the gaster is all black, but it is red in some specimens (red in *montanus*, all or basally). Individuals with a red gaster have forefemoral punctures three to five diameters apart between the notch and the apex (punctures about one diameter apart in *montanus*). Some males of *aethiops* have a sparsely punctate midfemoral venter and a glabrous zone on the midtibial dorsum, features absent in other species.

Description.—Punctures less than one diameter apart on frons and vertex. Vertex width more than length. Mesopleuron opaque, with conspicuous, somewhat irregular microsculpture. Propodeal dorsum regularly microareolate; side with conspicuous microsculpture, sometimes densely, indistinctly ridged; hindface finely ridged. Sternum I without apicomedian depression. Midtibia posteroexternally with impunctate zone which may be broad or narrow. Scutal and femoral setae appressed, scutal setae at middle oriented almost uniformly posterad. Hindcoxa not carinate.

Body black, including legs, or gaster red; tarsal apex reddish in male. Terga not fasciate. Wings infumate (strongly in female). Frontal vestiture silvery.

♀.—Clypeus (Fig. 8a): bevel longer than basomedian area; lip almost straight, with one lateral incision on each side, scarcely emarginate mesally in some specimens. Dorsal length of flagellomere I 2.1–2.7× apical width. Scutal punctures fine, but well defined, less than one diameter apart, except discal punctures (which are two to four diameters apart). Discal micropunctures of tergum II usually more than one diameter apart. Tergum V densely punctate, apical depression impunctate (at least mesally). Pygidial plate dull, shiny apically in some specimens, punctate and rugose (Fig. 8b) or (occasional specimens) rugae inconspicuous. Trochanteral venter shiny, finely, sparsely punctate. Fore- and midfemoral venter shiny, sparsely punctate (Fig. 8c, d). Length 11–13 mm.

Vertex setae subappressed, 0.3 MOD long, except erect, 0.6 MOD long, on postocellar impression. Vestiture not obscuring sculpture between antennal socket and orbit. Midfemoral venter practically glabrous. Outer face of foretibia and dorsum of mid- and hindtibia (sometimes narrowly) glabrous.

Figure 7 Geographic distribution of *Tachysphex montanus* (Cresson)

♂.—Mandibular inner margin with tooth (Fig. 8e). Clypeus (Fig. 8e, f): bevel shorter than basomedian area, evanescent in some specimens; lip arcuate, its corners obtuse; distance between lip corners equal to 0.8–1.0 of clypeal length and also of

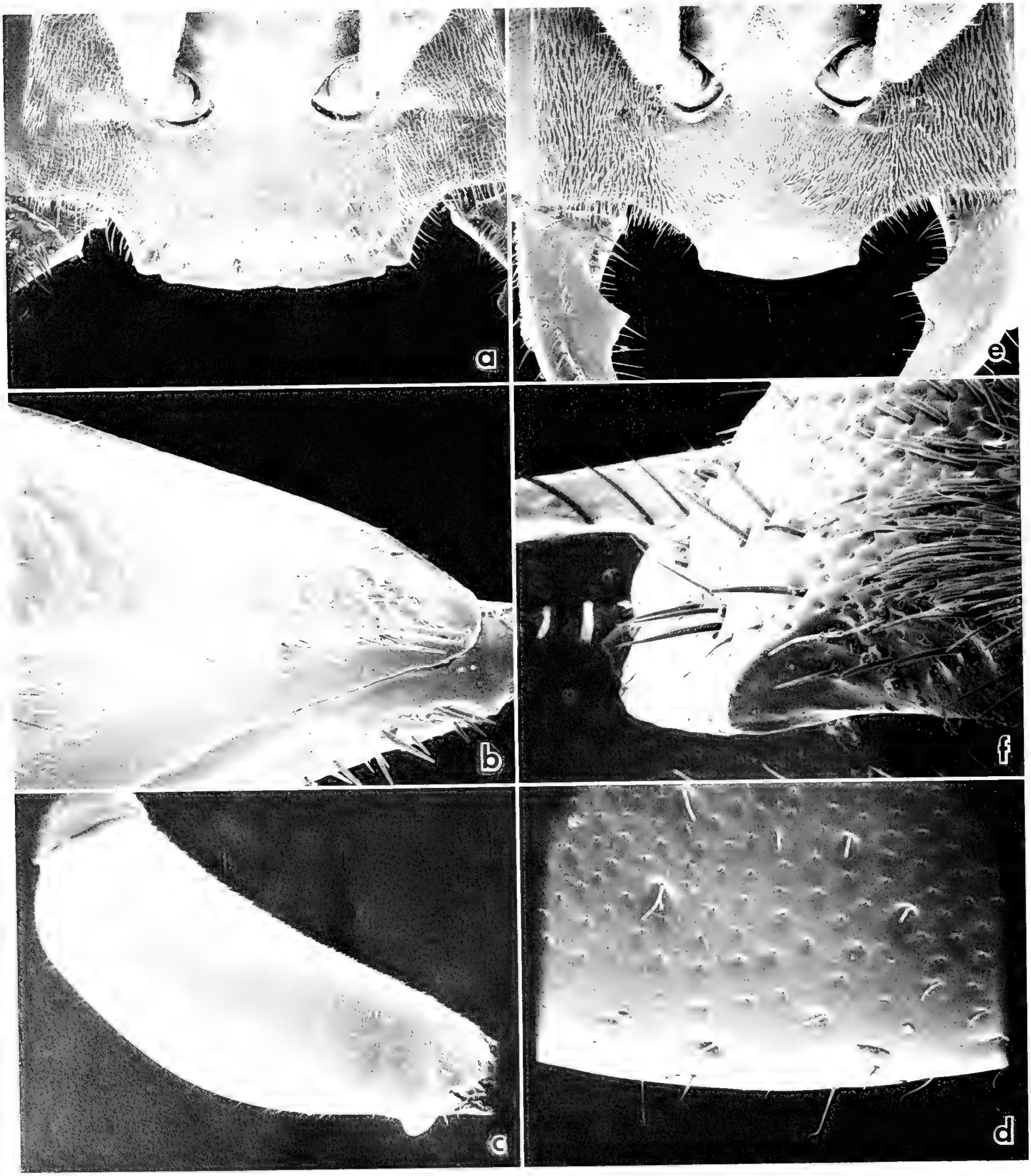

FIGURE 8. *Tachysphex aethiops* (Cresson). a—female clypeus, b—pygidial plate of female, c—female forefemur, d—sculpture of forefemoral venter of female, e—male clypeus, f—clypeal lobe of male, laterally.

TABLE 1. CHARACTERS ASSOCIATED WITH *TACHYSPHEX AETHIOPS*

Body part	*aethiops*	Specimens with red gaster
1) Gaster	Black	All red or (some females) segments III–IV black
2) Propodeal side	Microsculptured to finely ridged	Finely to coarsely ridged
3) Female pygidial plate	Punctatorugose or (some specimens) punctate	Punctate or (some specimens) weakly punctatorugose
4) Male forefemoral venter between notch and base	Punctures one to three diameters apart	Punctures three to five diameters apart

distance between corner and orbit; a sharp carina emerges from lip corners and extends slightly beyond lip base. Dorsal length of flagellomere I 1.2–1.7 × apical width. Vertex width 1.5–1.7 × length. Scutal punctures distinct, subcontiguous. Discal micropunctures of tergum II about one diameter apart. Sterna densely punctate throughout. Forefemoral notch glabrous. Foretarsus with one to four preapical rake spines; apical spine of tarsomere II equal to tarsomere III or much shorter. Midfemoral venter in many specimens shiny, sparsely punctate, glabrous (sometimes median third only), hindface more or less flattened or slightly concave. Length 8.0–10.5 mm.

Vertex setae erect, 1.0 MOD long. Integument largely obscured by vestiture between antennal socket and orbit.

VARIATION.—In the male, the trochanteral venter may be densely punctate or with only a few, sparse punctures; the punctures of the midfemoral venter are subcontiguous to sparse; the midtibia is densely punctate throughout or has a glabrous, dorsal zone.

DISCUSSION.—I am provisionally assigning to *aethiops*, as its red phase, specimens that closely resemble this species in most characters but that differ in gastral color, sculpture, and punctation as detailed in Table 1. Full intergradation has not been observed.

The gaster of the red form is all red in most specimens (dark reddish in a female from Sun Pass, Oregon; UCD). Segments IV–VI are black in a female from Osoyoos, British Columbia (CNC) and in a female collected 23 mi W Dillon, Montana (UCD).

LIFE HISTORY.—*Tachysphex aethiops* nests in flat, friable sand and in hard packed soil. Females dig their own nests (Evans 1970), but Alcock (1973) twice observed females entering open *Bembix* burrows; one remained inside the nest for over one hour, and the other modified a probable *Bembix* sleeping burrow for her nest. An active nest has two or three cells, and Evans (1970) noted a low, spreading mound of sand (8 cm wide by 5 cm long) in front of the nest entrance. The nest is oblique to the surface: the burrow length is 10–12 cm, and the cell is located at a depth of 4–6 cm. Recorded prey are immature Acrididae, *Trimerotropis* sp., probably *T. suffusa* Scudder, and only one is placed in a cell (Evans 1970, 1973; Alcock 1973). Prey length (12–20 mm) exceeded that of the wasp. The egg is attached to the forecoxal membrane of the hopper and extends transversely over the other forecoxa, with its posterior end free (Evans 1973).

Evans (1970) found a male of this species among the prey of *Philanthus pulcher* Dalla Torre.

GEOGRAPHIC DISTRIBUTION (Fig. 9).—The black form of *aethiops* ranges between Northwest Territories of Canada to southern California and central New Mexico. It is transcontinental in Canada and also occurs in the Great Lakes area and in Nebraska, but west of the 100th meridian in the remaining United States. The red form of *aethiops* occurs between southern British Columbia and southern Colorado, southern Arizona, and northern Baja California.

MATERIAL EXAMINED.—Black form: 415♀, 506♂; red form: 15♀, 36♂ (CNC, KU, LACM, UCD, UCR, UIM, USNM).

RECORDS (r: gaster red, all localities recorded).—CANADA: **Alberta:** Banff, Edmonton, Fort McMurray, Jumping Pd. Creek (20 mi W Calgary), 12 km SW Orion, Slave Lake, Writing-on-Stone Provincial Park. **British Columbia:** Graliano, Hell's Gate, Manning Provincial Park, Mt. Robson, Nicola, Osoyoos (r). **Northwest Territories:** Fort Providence, Fort Simpson, Fort Smith, Hay River, Rae, Yellowknife. **Ontario:** Kenora. **Quebec:** Tadoussac. **Saskatchewan:** Snowden, 5 mi E Swift Current.

UNITED STATES: ARIZONA: **Cochise:** Elfrida (r). **Coconino:** Grand Canyon (North Rim). **Maricopa:** 5 mi N Mesa (r). **Navajo:** Kayenta (r). **Pinal:** Apache Junction (r). CALIFORNIA: **Alpine:** Hope Valley (partly r) and five other localities. **Amador:** Ham's Station (Highway 880). **Calaveras:** Big Meadows. **Contra Costa:** Mt. Diablo. **El Dorado:** Strawberry (partly r) and nine other localities. **Fresno. Humboldt:** Big Lagoon, 1 mi S Blue Lake, 10 mi S Orick. **Inyo. Lassen:** Hallelujah Junction (r) and four other localities. **Madera:** Green Mt. (SE slope). **Modoc. Mono:** Mammoth Lakes (partly r), White Mts. (partly r) and seven other localities. **Nevada. Placer. Plumas:** Bucks Lake, 6 mi E Chester, Johnsville, Meadow Valley. **Riverside:** 10 mi NW Cottonwood (r), Hopkins Well (r). **San Bernardino:** 18 mi E Amboy (r), Dollar Lake trail, Fish Creek, Vidal Junction (r). **San Diego:** Borrego Springs (r). **Shasta. Sierra. Siskiyou. Trinity:** 10 mi W Coffee Creek, Lower Mumbo Lake (NE corner of county). **Tulare. Tuolumne. Ventura:** Hungry Valley (5 mi S Gorman, r). COLORADO: **Boulder. Chaffee:** Middle Cottonwood Creek in Sawatch Mts., Poncha Springs. **Clear Creek:** Chicago Creek, Loveland Pass, Mt. Evans (Dolittle Ranch). **Costilla:** Ute Creek (r). **Gunnison:** Gothic, Jack's Cabin (15 mi SE Crested Butte), Ohio. **Lake:** Leadville. **Larimer. Ouray:** Ouray. **Mesa:** 31 mi N Mack. **Mineral:** Creede, South Clear Creek. **Routt:** 15 mi S Steamboat Springs. **Teller:** Florissant. Also: locality unknown (r). IDAHO: **Bear Lake:** 5 mi W Ovid, Paris. **Bingham:** Taber (r). **Blaine:** Alice Lake (Sawtooth Mts.), Galena Summit. **Boise:** Garden Valley. **Boundary:** Highway 95 (3 mi S British Columbia). **Butte:** Bear Pass, Craters of the Moon National Monument (partly r). **Canyon:** 7 mi S Nampa. **Clark:** 3 mi NW Kilgore. **Clearwater:** Elk River. **Custer:** Bonanza, Farley Lake (Sawtooth Mts.). **Idaho:** 25 mi E Lowell. **Kootenai:** Lane. **Latah:** 2 mi E and 5 mi N Bovill. **Lincoln:** Shoshone (r). **Owyhee:** Murphy Hot Springs (r), 4 mi NE Reynolds (r). **Shoshone:** 7 mi E Avery. **Teton:** 4 mi W Tetonia, Victor. **Valley:** 2 mi SE McCall. MICHIGAN: **Alger:** Pictured Rocks National Lakeshore. **Marquette:** Huron Mountain Club. MINNESOTA: **Carlton:** Sawyer. MONTANA: **Beaverhead:** 23 mi W Dillon (r). **Madison:** 9 mi N Ennis. **Ravalli:** Hamilton. NEBRASKA: **Thomas:** 2.5 mi W Halsey. NEVADA: **Carson City. Douglas:** Spooners Lake N Junction Highway 28. **Elko:** 7 mi S Carlin (r) and five other localities. **Eureka:** Eureka. **Storey:** Virginia City (r). **Washoe:** Galena Creek, Incline Village, Mt. Rose. **White Pine:** Mt. Wheeler, Snake Creek. NEW MEXICO: **Sandoval:** Jemez Springs. **Santa Fe:** Little Tesuque Canyon. OREGON: **Baker:** Cornucopia. **Grant:** Antelope Mt. **Hood River:** Mt. Hood. **Klamath:** Crater Lake Park (Pole Bridge Meadow), 4 mi N Crescent, Lake of the Woods, Sun Pass (r). **Lake:** Hart Mt. Reserve. **Union:** North Powder. **Wallowa:** Hat Point. SOUTH DAKOTA: Black Hills National Forest. UTAH: **Cache. Daggett:** Hideout Canyon near Manila. **Garfield:** Blue Spruce Camp (18 mi N Escalante), 15–16 mi N Boulder. **Rich:** Logan Canyon summit, Monte Cristo, Park City. **Sanpete:** Flat Canyon Camp (33 mi NW Huntington). **Uintah:** Little Brush Creek (25 mi N Vernal), N Fork Duchesne River. **Weber:** Willow Flat. WASHINGTON: **King:**

FIGURE 9. Geographic distribution of *Tachysphex aethiops* (Cresson)

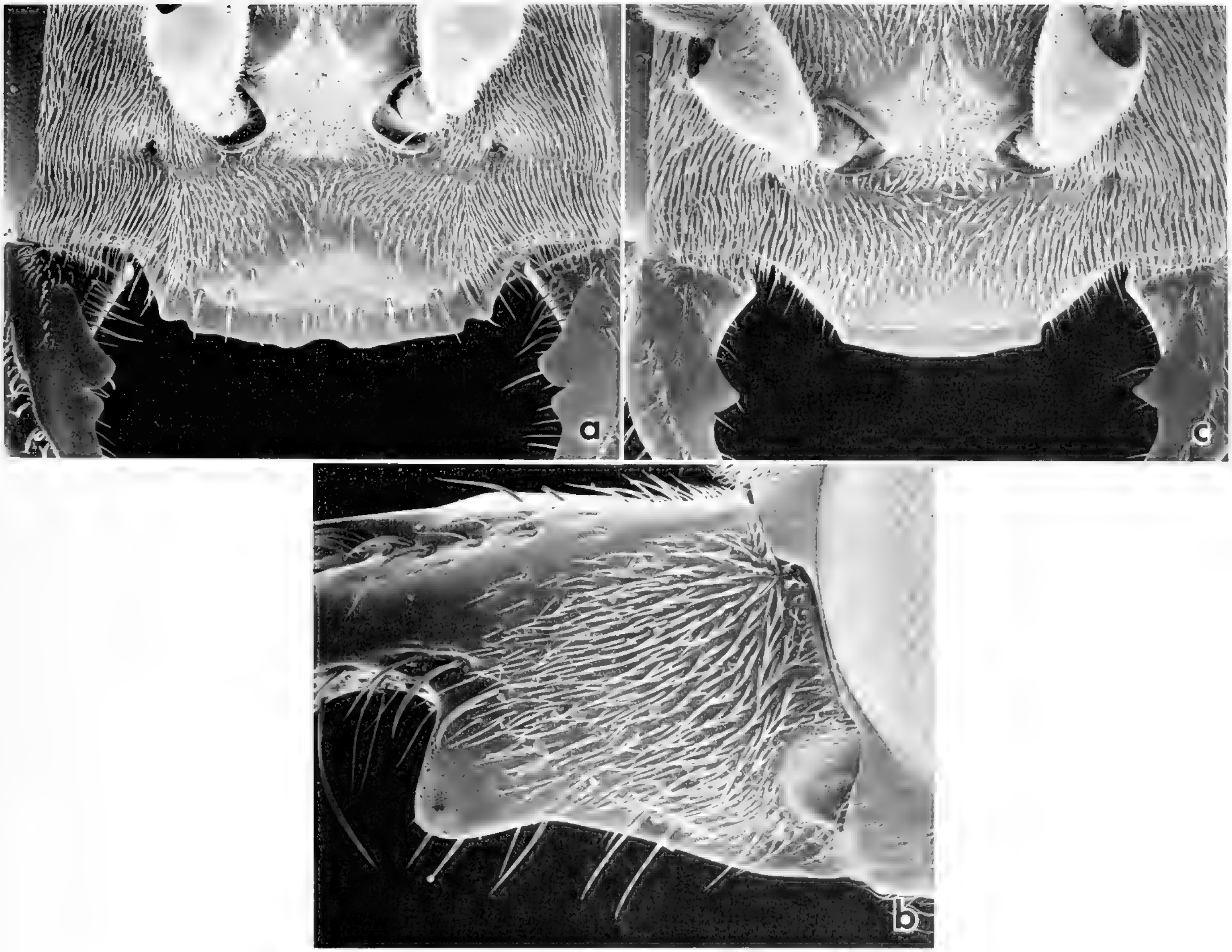

FIGURE 10. *Tachysphex orestes* sp. n.: a—female clypeus; b—female mandible; c—clypeus of presumed male

Seattle. **Kittitas:** Cooper Lake. **San Juan:** Friday Harbor. **Thurston:** Olympia. **Yakima:** Yakima. WYOMING: **Albany:** Summit. **Fremont:** Shoshone National Forest. **Park:** Lake Creek Camp (13 mi SE Cooke City), Sunlight Basin N Cody. **Sheridan:** Big Horn, Big Horn National Forest. **Sublette:** Pinedale, Sacajawea Camp (24 mi W Big Piney). **Teton.**

MEXICO: **Baja California Norte:** near La Zapopita in Valle de Trinidad (r)

Tachysphex orestes sp. n.

(Figures 10, 11)

DERIVATION OF NAME.—Orestes is a Greek word meaning mountaineer; noun in apposition.

DIAGNOSIS.—*Tachysphex orestes* has a dull, unevenly microsculptured mesopleuron. The female can be recognized by the following combination of characters: clypeal lip incised laterally, shallowly emarginate mesally; venter of mid- and hindtrochanters shiny, in most specimens impunctate or sparsely punctate; mesopleural setae suberect on hypoepimeral area and appressed or nearly so beneath the scrobe; and gaster all red (at least the sterna). Unlike *eldoradensis*, the setae of the postocellar impression are shorter than 0.5 MOD (about 1.0 MOD long in that species), and the silvery tergal fasciae are well defined (inconspicuous in *eldoradensis*). In addition, the mandibular ventral margin of *orestes* is convex basally (Fig. 10b) and the vertex width is 1.2–1.4× length, while in *eldoradensis* the mandibular ventral margin is straight basally in many specimens, and the vertex width is 1.4–1.6× length.

DESCRIPTION.—Mandibular ventral margin sinuate between base and notch (convex near base), but weakly so in some specimens. Punctures less than one diameter apart on frons, vertex, and scutum. Mesopleuron microsculptured, at most with ill-defined punctures. Mesothoracic venter densely punctate. Propodeal dorsum microareolate, side microsculptured, in some specimens also partly microridged; hindface finely ridged. Sternum I without apical depression. Hindcoxa not carinate or with rudimentary basal carina.

Setae not concealing integument between antennal socket and orbit, appressed on vertex, uniformly oriented posterad on scutum, nearly erect on hypoepimeral area, appressed or nearly no beneath mesopleural scrobe, diverging anterad on propodeal dorsum.

FIGURE 11 Geographic distribution of *Tachysphex orestes* sp. n.

Head, thorax, and legs black (tarsomeres II–V or III–V ferrugineous), gaster red in most specimens, but apical terga black in single female from British Columbia. Terga I–III fasciate apically. Wings moderately infumate. Frontal pilosity silvery.

♀.—Clypeus (Fig. 10a): bevel longer than basomedian area; lip arcuate, incised laterally, notched mesally (notch evanescent in some specimens, absent in worn specimens). Dorsal length of flagellomere I 2.2–2.4 × apical width. Vertex width 1.2–1.4 × length. Discal micropunctures of tergum II evanescent, two to three diameters apart. Tergum V: punctures averaging two to three diameters apart mesally; apical depression impunctate. Pygidial plate shiny, punctate. Femora finely, uniformly punctate. Trochanteral venter shiny, impunctate or with sparse, inconspicuous punctures (fore- and midtrochanter densely punctate in some specimens). Length 7.5–10.0 mm.

♂.—Unknown. The clypeus of a male that probably belongs to this species is shown in Figure 10c.

DISCUSSION.—*Tachysphex orestes* is common in many places in the Sierra Nevada, California, and many males must have been represented in the material I have studied. Nevertheless, I have not been able to clearly distinguish them from males of some other phena that still remain undefined. As a result, the male of *orestes* has not been included in the present revision.

GEOGRAPHIC DISTRIBUTION (Fig. 11).—Montane areas between British Columbia and Baja California Norte, east to Idaho, Wyoming, and central Arizona.

COLLECTING PERIOD.—13 May (Baja California Norte), 23 May–5 August (United States and Canada).

MATERIAL EXAMINED.—Holotype: ♀, California: Placer: Carnelian Bay, 10 July 1975, WJP (CAS, Type #15906).

Paratypes (236♀): CANADA: **British Columbia:** Skihist Camp near Lytton (on Frazer River), EIS (1♀, UCD)

UNITED STATES: ARIZONA: **Coconino:** Ft. Valley (Flagstaff), collector unknown (1♀, UCD). CALIFORNIA: **Alpine:** Hope Valley, PDH, JWMS (2♀, UCD); Red Lake, MEI (2♀, UCD); 1.5 mi NE Red Lake, EIS (1♀, UCD); no specific locality, A. C. Browne (1♀, LACM). **Amador:** Ham Station, F. E. Strong (1♀, UCD). **Calaveras:** Big Meadow, ASM (1♀, UCD). **El Dorado:** Blodgett Forest (18 mi E Georgetown), JAP (2♀, CIS) and JWMS (1♀, CIS); Echo Lake, J. C. Downey (1♀, UCD); Fred's Place, R. O. Schuster (1♀, UCD); 8 mi NE on Icehouse Road, R. B. Kimsey (1♀, UCD), WJP (3♀, CAS); Kyburz, S. C. Kuba (2♀, CAS); Meyers, MEI (1♀, UCD). **Fresno:** Deadman Canyon in Kings Canyon National Park, R. E. Rice (1♀, UCD); Huntington Lake, L. McCracken (1♀, UCD). **Inyo:** Big Pine Creek, RMB, FDP (2♀, UCD). **Kern:** Mt. Pinos, JAP (1♀, CIS). **Lassen:** Hallelujah Junction, MEI, J. A. Miller (3♀, UCD); Susanville, TRH (5♀, CSDA). **Los Angeles:** Blue Ridge in San Gabriel Mts., R. R. Snelling (1♀, LACM). **Modoc:** 5 mi NE Alturas, TRH (1♀, CSDA); 14 mi N Alturas, V. L. Vesterby (1♀, UCD); Cedar Pass, D. L. Dahlsten (1♀, UCD), collector unknown (1♀, CNC); Fandango Pass, TRH (1♀, CSDA). **Mono:** Cottonwood Creek, G. I. Stage, G. W. Frankie (2♀, CIS); Crowley Lake, O. C. Lafrance (1♀, LACM); Parker Creek 8 mi S Lee Vining, WJP (1♀, CAS); White Mts. (Blanco Corral), JWMS (2♀, UCD). **Nevada:** Boca, RMB, PMM (2♀, UCD), WJP (1♀, WJP); Hobart Mills, RMB (1♀, UCD); Russell Valley, J. A. Froebe (1♀, UCD); Sagehen Creek near Hobart Mills, RMB, R. C. Blaylock, R. L. Brumley, M. A. Chambers, DSH, MEI, L. S. Kimsey, JAP (3♀, BMNH; 4♀, CAS; 26♀, UCD), M. C. Axtman (1♀, LACM), WJP (1♀, WJP); 7 mi SE Truckee, RMB (2♀, UCD). **Placer:** Carnelian Bay on Lake Tahoe, RMB, B. Villegas (23♀, UCD; 3♀, USNM), WJP (1♀, CAS), W. Turner (2♀, WSU); Dollar Point 2 mi NE Tahoe City, P. Adams (3♀, CSDA); Lake Tahoe, collector unknown (1♀, UCD); Nyack (12 mi W Emigrant Gap), WJP (1♀, CAS); Serene Lakes 3–4 mi S Soda Springs, P. Buickerood (2♀, CAS); Tahoe, FXW (5♀, UCD). **Plumas:** Bucks, collector illegible (2♀, UCD); 6 mi E Chester, RMB (2♀, UCD); 14 mi W Johnsville, M. R. Gardner (2♀, UCD). **Riverside:** Pine Cove (San Jacinto Mts.), E. S. Ross (1♀, UCD). **San Bernardino:** Fish Creek in San Bernardino Mts., KWC (1♀, CAS). **San Diego:** Corte Madera, DKF (1♀, SDNH); Laguna Mts., R. B. Parks (1♀, SDNH); Mount Laguna, PDH (1♀, CIS) and JAP (1♀, CIS); Mount Palomar, R. L. Langston (1♀, CIS). **Shasta:** Hatchet Mt. Pass, TRH (1♀, CSDA), 5 mi NE Old Station (4♀, CSDA). **Sierra:** Gold Lake, C. L. Fox, G. A. Schaefers (2♀, UCD), HKC (1♀, CAS); Independence Lake, RMB, R. L. Brumley, JAP (5♀, UCD); Packer Lake, R. L. Westcott (1♀, UCD); Sierra Buttes, E. J. Montgomery (2♀, UCD); Sierraville, FDP (1♀, UCD); Yuba Pass, RMB, MEI, L. S. Kimsey, E. J. Montgomery (6♀, UCD) **Siskiyou:** Ash Creek Ranger Station (9 mi E McCloud), REC (2♀, UCD); Ash Creek Ranger Station at McCloud River, WWM (1♀, CIS); 3 mi E Ash Creek Ranger Station, REC (1♀, CIS) and J. Doyen (1♀, CIS); Dorris, WJP (1♀, CAS); Lower Devil's Peak, TLG (1♀, TLG); 3 mi N Medicine Lake, J. Schuh (1♀, UCD);

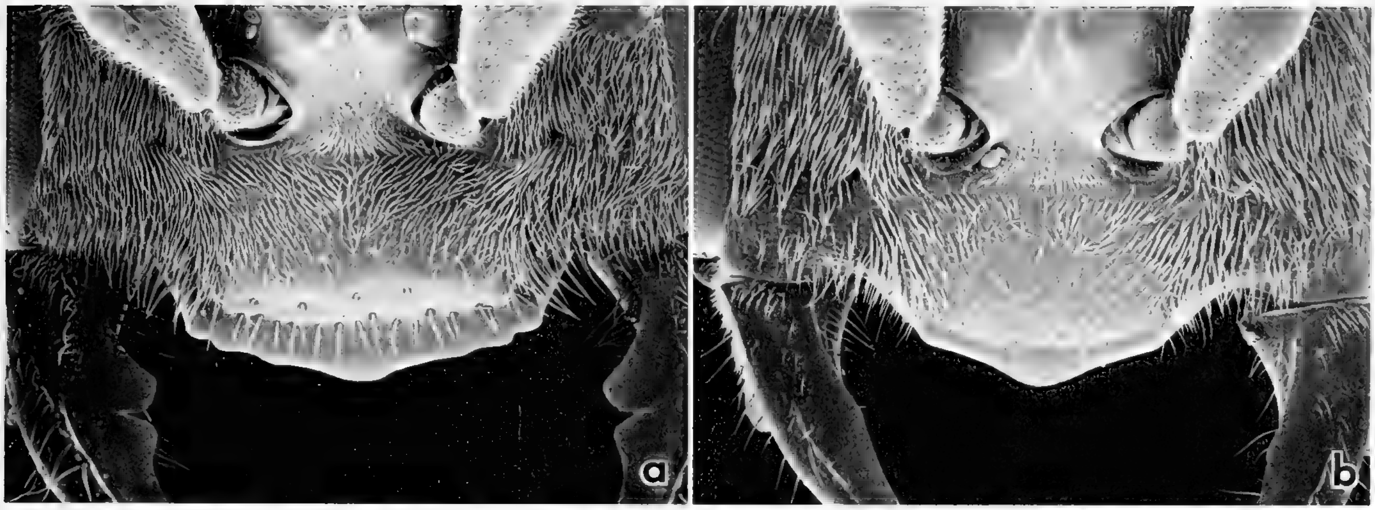

FIGURE 12. *Tachysphex angelicus* sp. n.: a—female clypeus; b—male clypeus.

Mt. Shasta town, JAP (1♀, CIS), WJP (3♀, CAS). **Trinity:** Coffee Creek 10 mi W Ranger Station, RMB (1♀, UCD); 10 mi N Coffee Creek Ranger Station, JWMS (2♀, CIS). **Tulare:** Nine Mile Canyon (5 mi E Smith Meadow), C. W. O'Brien, Potwisha (junction of Marble and Middle forks of Kaweah River), E. C. Van Dyke (1♀, UCD). **Tuolumne:** Kennedy Meadow, R. H. James (1♀, UCD); Strawberry, RMB, A. T. McClay, W. T. Crites, R. H. James, EGL (7♀, UCD). COLORADO: **County unknown:** MacDoel, J. Schuh (2♀, UCD). IDAHO: **Bear Lake:** Montpellier, collector unknown (1♀, AMNH). **Fremont:** St. Anthony Sand Dunes, MSW (2♀, CSDA). **Oneida:** 5 mi NW Holbrook, W. J. Hansen (2♀, USU). **Teton:** Grand Teton, collector unknown (1♀, UCD). **Twin Falls:** Castleford, collector unknown (1♀, USNM). NEVADA: **Douglas:** Genoa, FDP (2♀, UCD). **Elko:** 7 mi NE Carlin, FDP (1♀, UCD). **Humboldt:** Paradise Valley, FDP (1♀, UCD); Santa Rosa Ranch, ASM (1♀, UCD). **Lander:** Austin, RMB (1♀, UCD). **Washoe:** 21 mi SE Eagleville, California, P. Opler (1♀, CIS); Mt. Rose (Galena Creek), RMB (2♀, UCD), FDP (1♀, NSDA); 4 mi W Wadsworth, R. B. Miller (1♀, FSDA). **White Pine:** 34 mi W Ely, RMB (1♀, UCD). OREGON: **Deschutes:** Tumalo Reservoir, EIS (1♀, UCD). **Klamath:** Crater Lake National Park, Schuh, Hansen, and Miller (1♀, UCD); Eagle Ridge (Klamath Lake), C. L. Fox (1♀, UCD); base of Mt. Pitt, Vertrees and Schuh (1♀, UCD); Lake of the Woods, H. A. Scullen (1♀, UCD); Sand Creek near Crater Lake, J. Schuh (4♀, UCD). **Lake:** Warner Lake, E. C. Van Dyke (1♀, UCD). **Wallowa:** Lick Creek Ranger Station in Wallowa National Forest, D. Bolinger and S. G. Jewett (1♀, OSU). UTAH: **Bonanza:** SW Bonanza, 1524–1706 m, M. Schwartz (1♀, CAS; 1♀, USU). **Box Elder:** 15 mi W Snowville, J. Hansen (1♀, USU). **Cache:** Blacksmith Fork Canyon, W. J. Hansen (1♀, CAS; 2♀, USU). **Emery:** Orange Olsen Ranger Station, P. K. Cowley (2♀, CAS; 2♀, USU). **Rich:** Logan Canyon summit, Malaise trap (1♀, USU). WYOMING: **Park:** Sunlight Basin N Cody, GEB (1♀, UCD). **Sweetwater:** Green River, collector unknown (2♀, AMNH, UCD).

MEXICO: **Baja California Norte:** 1 mi S El Cóndor, JWB and DKF (1♀, SDNH)

Tachysphex angelicus sp. n.

(Figures 12, 13)

DERIVATION OF NAME.—Angelicus is a Latin masculine adjective derived from angelus, an angel; with reference to the Los Angeles area of California, where most specimens have been collected.

DIAGNOSIS.—The female of *angelicus* can be recognized by the shape of the clypeal lip, which is obtusely triangular mesally (Fig. 12a). Some *spatulifer* are similar, but in that species the lip surface has several shallow concavities (lip surface flat or nearly so in *angelicus*) and the midflagellar articles are shorter (e.g., the length of flagellomere II is 3.0–3.4× width in *angelicus* and 2.3–2.4 in *spatulifer*). Unlike *tahoe,* which is somewhat similar, the vertex setae of *angelicus* are markedly inclined (erect in *tahoe*), and the body length is 12.5–13.0 mm (6.5–8.0 mm in *tahoe*).

The male of *angelicus* has an obtusely triangular or markedly sinuate clypeal lip (Fig. 12b), almost nondentate mandible, a dull mesopleuron with ill-defined punctures, nearly appressed vertex setae, the midscutal setae oriented posterad, and finely, uniformly setose sterna. Other species are similar, but they differ as follows: vertex setae erect in *mirandus, psammobius, tipai,* most *tahoe,* and some *crenulatus*; sterna II–IV largely glabrous in *mirandus*; sterna III and IV velvety pubescent in *musciventris* and *tahoe.* Most similar are *crenulatus* and *spatulifer,* but their midflagellar articles are shorter than in *angelicus*; e.g., the length of flagellomere II is 1.6–1.8× width in these two species, but 2.0–2.2× in *angelicus.* Furthermore, the clypeal lip corners of *angelicus* are closer to orbits than to each other (closer to each other than to orbits in *crenulatus*), and the trochanteral venter of *angelicus* is densely punctate (sparsely punctate in most *crenulatus*).

DESCRIPTION.—Punctures nearly contiguous on frons below midocellus, scutum, and mesothoracic venter; on vertex nearly contiguous in male, locally up to one or two diameters apart in some females. Mesopleuron dull, microsculptured, with shallow, ill-defined punctures. Propodeal dorsum evenly microareolate; side ridged in most females (ridges evanescent in the specimen from Walker Spring), evenly microsculptured or microridged in male; hindface ridged. Sternum I without apical depression.

Integument not entirely concealed by vestiture between antennal socket and orbit. Setae: on vertex markedly inclined anterad but not appressed, up to 0.7 MOD long; on midscutum oriented posterad; on mesopleuron markedly inclined but not appressed; on propodeal dorsum oriented obliquely anterad (divergent anterad); on midfemoral venter appressed or nearly so.

Head, thorax, and legs black, tarsal apex reddish (inner face of hindfemur reddish in single female from Plumas County). Gaster red or (some males) terga V–VII black. Frontal vestiture silvery. Terga I–III silvery fasciate apically. Wings weakly infumate.

♀.—Clypeus (Fig. 12a): bevel about as long as basomedian area; lip arcuate, obtusely triangular mesally, undulate laterally.

FIGURE 13. Geographic distribution of *Tachysphex angelicus* sp. n.

Dorsal length of flagellomeres I and II 2.3–2.5 and 3.0–3.4 × apical width, respectively. Vertex width 0.9–1.2 × width. Tergum V with scattered punctures, its apical depression impunctate. Pygidial plate alutaceous, shiny, sparsely punctate. Trochanteral venter finely, densely punctate. Length 7.5–12.0 mm.

♂.—Mandibular inner margin practically not dentate (Fig. 12b), tooth reduced to a small, very obtusely angulate projection. Clypeus (Fig. 12b): bevel ill defined; lip obtusely angulate or markedly sinuate, its corners ill defined, separated by a distance equal to 1.0–1.1 of clypeal length and to about 1.1 of distance between corner and orbit. Dorsal length of flagellomeres I and II 1.4–1.7 and 2.0–2.2 × apical width, respectively. Sternal punctures slightly finer than those on mesothoracic venter. Forefemoral notch pruinose. Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II shorter than tarsomere width. Length 5–9 mm.

LIFE HISTORY.—The holotype female was collected on flowers of *Eriogonum fasciculatum* Benth.

GEOGRAPHIC DISTRIBUTION (Fig. 13).—Southeastern Arizona, California, and adjacent areas of southwestern Nevada.

COLLECTING PERIOD.—10 April to 22 July.

MATERIAL EXAMINED.—Holotype: ♀, California: San Diego Co.: 1 mi S Del Mar, 1 July 1963, PDH (CIS, on indefinite loan to CAS, CAS Type #15902).

Paratypes (27♀, 16♂): UNITED STATES: ARIZONA: **Cochise:** Huachuca Mts. 15 mi S Sierra Vista, 21 May 1967, Sternitzky (1♀, CNC). CALIFORNIA: **Los Angeles:** Little Rock, 21 May 1966, collector unknown (1♀, LACM); Llano, 1 June 1957, W. F. Simonds (1♀, UCD), Tanbark Flat, 25 June and 16 July 1956, RMB (1♂, CAS; 2♂, UCD), Wrightwood, 82 E 31 (–31 May 1982), KWC (1♀, CAS). **Mono:** 11 mi N Bridgeport, 7 July, RMB (1♂, UCD); Mammoth Lake, 22 July 1936, RMB and GEB (1♀, UCD). **Plumas:** Little Long Valley (6 mi E Spring Garden), 6–10 Aug, MSW (1♀, CSDA). **Riverside:** Pinyon Flats, 13 June 1966, WWM and D. C. F. Rentz (1♀, CIS). **San Bernardino:** 1 mi S Adelanto, 1 June, MEI (1♀, CAS), Cajon, 17 and 19 July 1956, RCB (2♂, CAS, UCD), 17 July 1956, H. R. Moffitt (1♀, CAS); 4.3 mi NNW Granite Pass, 24 May 1983, TLG (1♀, USU), 10 mi N Lake Arrowhead, 15 June 1960, P. E. Paige (1♀, UCD). **San Diego:** 1 mi S Del Mar, 1 July 1963, C. H. Frady (1♀, OSU), Encinitas, 6 June 1934, H. L. McKenzie (1♂, UCD), Borrego Valley (Palm Canyon), 10 Apr 1957, R. W. Bushing (1♀, CAS). **Santa Barbara:** Bluff Camp in San Rafael Mts., 29 June 1959, RMB (1♀, UCD). **Tulare:** Whitney Portal, Wylie (1♀, SDNH). **Ventura:** Hungry Valley (5 mi S Gorman), 4 May 1959, PDH (1♂, CIS), and 6 May 1959, C. W. O'Brien (2♂, CAS, 2♂, CIS), Wagon Road No. 2 Campground (18 air mi WSW Gorman), 4 and 5 July 1968, PHA (5♀, 10♂ CAS). NEVADA: **Esmeralda:** Walker Springs (circa 37°22'N, 117°37'W), HKC, 3 July 1960 (1♀, UCD).

Tachysphex acutus (Patton)

(Figures 14, 15)

Larra acuta Patton, 1881:390, ♂. Syntype ♂♀: Connecticut: New Haven Co.: Waterbury (destroyed). Neotype: ♂: Connecticut, Litchfield Co.: Colebrook, August 1918, W. M. Wheeler (MCZ), **present designation.**—Patton 1881:388, Kohl 1885:240.—In *Tachysphex*: Fox 1894*a*:521; Dalla Torre 1897:677; Ashmead 1899:250, H. Smith 1908:380; J. Smith 1910:683, Williams 1914:171, Rohwer 1916:687, Mickel 1918:423, Robertson 1928:71, 92, 121, 128, 163, 195, 201; Brimley 1938:443; G. Bohart 1951:950, Bohart and Menke 1976:272; Krombein 1979:1627, Finnamore 1982:101.

Tachysphex bruesi Rohwer, 1911:577, ♂. ! Holotype: ♂, Wisconsin: Milwaukee Co.: no specific locality (USNM). Synonymized by G. Bohart 1951:950.

Tachysphex sepulcralis: Krombein 1958*a*:52 (!)

DIAGNOSIS.—*Tachysphex acutus* differs from other *Tachysphex* (except *punctifrons*, in which the subalar fossa is carinate below) in having an angulate inflexion or weak carina between the dorsal end of the postspiracular carina and the anterior end of the subalar carina (Fig. 14b) and also a longitudinal, broad keel on the basal half of sternum I (Fig. 14c). The black body, the dull, impunctate (at least posteriorly) mesopleuron, and nonfasciate tergum IV are subsidiary diagnostic characters.

DESCRIPTION.—Frons, vertex, and scutum punctate; frontal punctures subcontiguous; vertex and scutal punctures subcontiguous or (some individuals) some punctures slightly more than one diameter apart. Mesopleuron dull, densely, shallowly punctate in anterior half (almost entirely so in certain males). Subalar

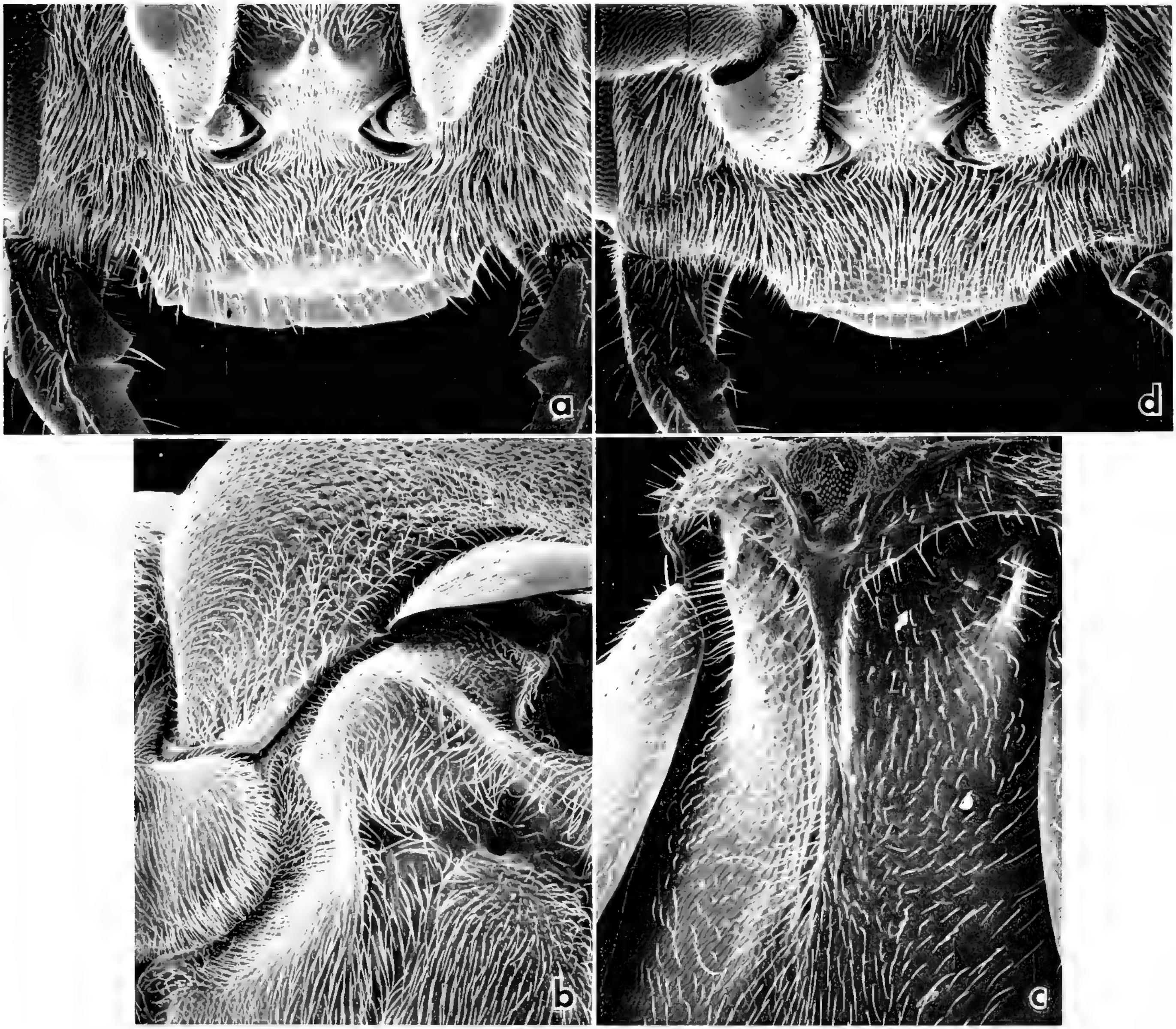

FIGURE 14. *Tachysphex acutus* (Patton): a—female clypeus; b—pronotal lobe and anterior part of female mesothorax; c—female sternum I; d—male clypeus

fossa delimited anteriorly by an angulate inflexion or weak carina that extends between postspiracular carina and anterior end of subalar carina (Fig. 14b). Propodeum dull, dorsum microareolate, usually also ridged or rugose, side ridged (ridges indistinct in some females, evanescent in certain small males), hindface ridged. Discal micropunctures of tergum II one to two diameters apart. Sternum without apical depression, its basal half with broad, mesal keel (Fig. 14c). Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit. Vertex setae 0.5 MOD long, suberect (female) or erect (male); scutal setae 0.5–0.6 MOD long, at middle oriented almost uniformly posterad; midfemoral venter with appressed setae.

Body black. Terga I–III silvery fasciate apically. Wings weakly infumate. Frontal vestiture silvery.

♀.—Clypeus (Fig. 14a): bevel slightly shorter than basomedian area; lip arcuate, indented laterally. Dorsal length of flagellomere I 1.7–2.1 × apical width. Vertex wider than long. Tergum V densely punctate, apical depression usually impunctate. Pygidial plate shiny, sparsely punctate. Trochanteral and femoral punctation fine, dense. Length 7.5–9.0 mm.

♂.—Mandibular inner margin with tooth (Fig. 14d). Clypeus (Fig. 14d): bevel equal to basomedian area or much shorter; lip arcuate or sinuate; lip corners rectangular to obtuse, closer to each other than to orbit (ratio: 1:1.3–1.4). Dorsal length of flagellomere I 1.3–1.6 × apical width. Vertex width 1.4–1.9 × width. Sterna densely punctate throughout. Forefemoral notch glabrous. Foretarsus without rake; outer apical spine of foretarsomere II shorter than tarsomere width. Length 5.0–6.5 mm.

DISCUSSION.—According to F. E. Kurczewski (pers. comm.), who obtained his information from J. C. Bradley and E. C. Zimmerman, the three syntypes of *Larra acuta* Patton were destroyed in a fire at the Boston Museum of Natural History around the turn of the century. However, the original diagnosis

FIGURE 15. Geographic distribution of *Tachysphex acutus* (Patton).

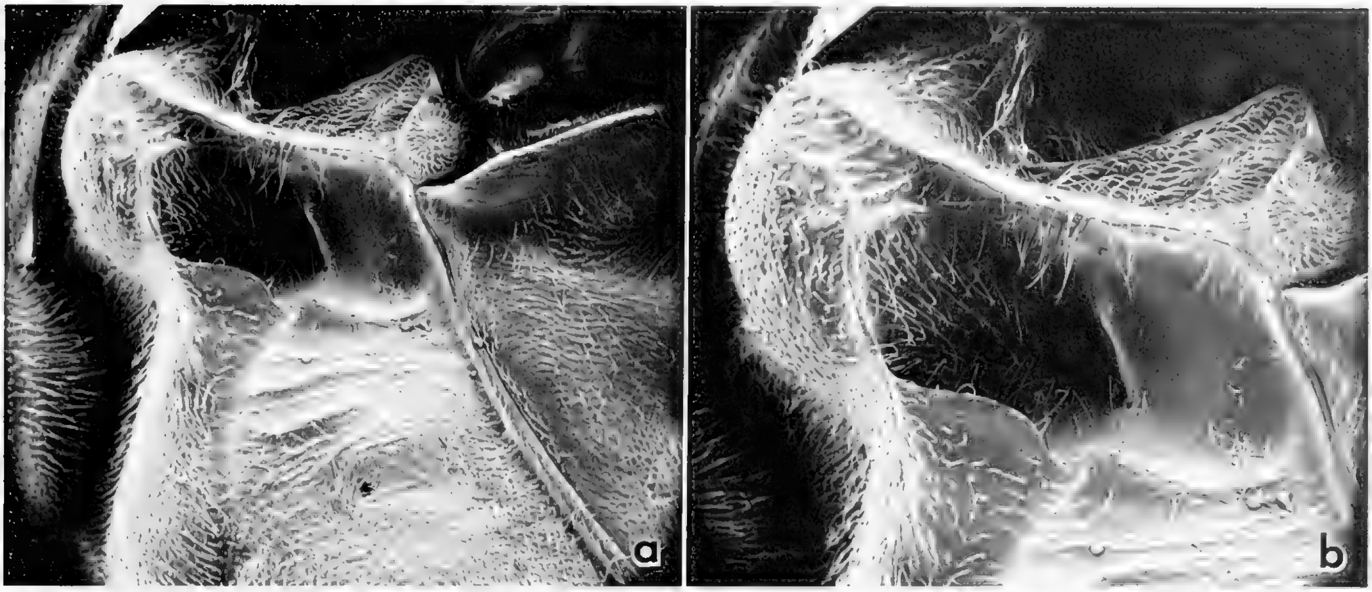

FIGURE 16. *Tachysphex punctifrons* W. Fox, female: a—upper mesopleuron; b—subalar fossa.

agrees rather well with the present species. First, Patton (1881) says that "it is related to *terminata, tarsata* and *montana,*" and this means that it actually is a *Tachysphex*. Second, the black body and silvery fasciate terga I–III noted by Patton are found only in two *Tachysphex* species in New England: *punctifrons* and this species. The body length given by Patton (8–9 mm) excludes *punctifrons*. There is, however a discrepancy between his description and the present species in the sculpture of the propodeal dorsum and side: they are "uniformly and finely granulated" according to Patton, while the side is ridged in all the females studied by me (although ridges are sometimes indistinct). Despite this difference I have designated a neotype that corresponds to the traditional interpretation of *T. acutus*.

LIFE HISTORY.—Robertson's (1928) floral records are unreliable because I suspect he misidentified the species. He recorded *acutus* from flowers of *Chamaecrista fasciculata* (Michx.) Greene (as *Cassia chamaecrista* (L.)), *Ceanothus americanus* L., *Cicuta maculata* L., *Eupatorium perfoliatum* L., *Heracleum lanatum* Michx., *Pycnanthemum flexuosum* (Walt.) B.S.P., and *Solidago canadensis* L.

GEOGRAPHIC DISTRIBUTION (Fig. 15).—North America east of 100th meridian, north to New Brunswick and southern Manitoba, south to northern Florida and Kansas.

MATERIAL EXAMINED.—127♀, 65♂

RECORDS.—CANADA: **Manitoba:** 5 mi SW Shilo. **New Brunswick:** Nerepis, St John. **Ontario:** Chatterton, Marmora, Orrville, Sillsville

UNITED STATES: CONNECTICUT: **Hartford:** Hartford. **Litchfield:** Colebrook. **New Haven:** Waterbury (Patton 1881). DISTRICT OF COLUMBIA: Washington. FLORIDA: **Alachua:** Gainesville. **Gadsden:** Quincy. ILLINOIS: Chicago. **Bureau:** Princetown. **Douglas:** Arcola. **McHenry:** Algonquin. IOWA: **Iowa:** —. **Palo Alto:** Ruthven. **Woodbury:** Sioux City. KANSAS: **Douglas:** Baldwin. **Leavenworth, Norton, Rice:** —. **Riley:** Manhattan. **Russell, Smith:** —. MARYLAND: **Montgomery:** Plummers Island. **Prince Georges:** Beltsville. MASSACHUSETTS: **Barnstable:** Sagamore. **Middlesex:** Bedford near Boston. **Nantucket:** Nantucket. **Worcester:** Petersham. MICHIGAN: **Alcona, Huron, Iosco:** —. **Lapeer:** Deerfield. **Livingston:** E. S. George Reserve. **Manistee, Mecosta:** —. **Washtenaw:** Ann Arbor, Stinchfield Woods. MINNESOTA: **Bluearth:** Mankato. MISSOURI **Boone:** Columbia. **St. Louis:** St. Louis. NEBRASKA: **Douglas:** Omaha. **Holt:** — **Lancaster:** Lincoln. NEW HAMPSHIRE: **Belknap:** Alton. **Rockingham:** Nottingham. **Strafford:** Durham. NEW JERSEY: **Burlington:** Riverton. **Mercer:** Princeton. NEW YORK: **Cayuga:** Auburn, Fair Haven, Mount Whiteface near Lake Placid. **Madison:** Chittenango. **Monroe:** Mendon Ponds. **Nassau:** Roslyn. **Oswego:** Mallory, Oswego. **Rensselaer:** Brainard. **Suffolk:** Bohemia. **Tompkins:** Ithaca, McLean. **Ulster:** Cherrytown near Kerhonkson. NORTH CAROLINA: **Cumberland:** Fort Bragg. **Duplin:** Wallace. **Macon:** Highlands. **Moore:** Southern Pines. OHIO: **Franklin:** Columbus. SOUTH CAROLINA: **Charleston:** McClellanville SOUTH DAKOTA: **Brookings:** Brookings. TENNESSEE: **Morgan:** Burrville VERMONT: **Windham:** Jamaica. **Windsor:** Hartland. VIRGINIA: **Fairfax:** Falls Church, Glencarlyn, Great Falls. **Stafford:** Stafford. WEST VIRGINIA: **Hardy:** Lost River State Park. WISCONSIN: **Milwaukee:** Milwaukee

Tachysphex punctifrons (W. Fox)

(Figures 16, 17)

Larra punctifrons W. Fox, 1891:194, ♀. ! Lectotype: ♀, Montana: no specific locality (USNM), **present designation.**—In *Tachysphex:* W. Fox 1894*a*:531 (♂); Dalla Torre 1897:684; Ashmead 1899:250; J. Smith, 1900:518, 1910:683; H. Smith 1908:380; Mickel 1918:423; Strickland 1947:129; G. Bohart 1951:952; Krombein and Evans 1954:231; Kurczewski 1971:114 (in key); Bohart and Menke 1976:276; Krombein 1979:1629; Kurczewski 1987:118

Tachysphex fedorensis Rohwer, 1911:576, ♀, ♂ ! Lectotype: ♀, Texas: Lee Co Fedor (USNM), **present designation.** Synonymized by G. Bohart 1951:952

DIAGNOSIS.—The following distinguish *punctifrons* from all other *Tachysphex*: upper mesopleuron longitudinally ridged, subalar fossa unusually deep and carinate below, and postspiracular carina of mesopleuron practically attaining the subalar carina (Fig. 16a, b).

DESCRIPTION.—Punctures less than one diameter apart on frons, subcontiguous on vertex and mesothorax. Mesopleuron longitudinally ridged above (Fig. 16a); subalar fossa carinate below (Fig. 16b), but carina interrupted by episternal sulcus; postspiracular carina much longer than in other species, almost reaching subalar carina; bottom of subalar fossa smooth, shiny, glabrous. Propodeal dorsum uniformly microareolate, side microsculptured, sometimes microridged. Terga densely microsculptured. Hindcoxa not carinate.

Scutal and midfemoral setae appressed, midscutal setae oriented obliquely posterad.

Body black, including legs (tarsal apex reddish in many males). Terga I–III silvery fasciate apically. Wings infumate (moderately so in male), with yellowish tinge.

♀.—Clypeus: bevel shorter to longer than basomedian area; lip incised laterally, usually emarginate mesally. Dorsal length of flagellomere I 2.4–2.8 × apical width. Vertex markedly wider than long. Tergum V densely punctate, including apical depression. Pygidial plate shiny, punctate. Trochanters finely, densely punctate. Forefemoral venter with fine, well-defined, subcontiguous punctures, but a few large punctures. Length 11–14 mm.

Vertex setae suberect, 0.3 MOD long mesally, 0.7 MOD long laterally. Vestiture inconspicuous, not obscuring integument between antennal socket and orbit.

♂.—Clypeus: bevel indistinct, much shorter than basomedian area; lip weakly arcuate, its lateral corners rectangular to obtuse, closer to each other than to orbit. Dorsal length of flagellomere I 1.7–2.1 × apical width. Vertex width 1.9–2.2 × length. Sterna punctate, pubescent, apical depression of sterna II–VI partly glabrous. Foretarsus without rake; outer apical spine of tarsomere II much shorter than tarsomere III. Length 8–13 mm.

Vertex setae erect, 1.0 MOD long anteriorly, several times shorter than MOD posteriorly. Vestiture concealing integument between antennal socket and orbit.

Life History.—Kurczewski (1987) observed nesting and provisioning behavior of *punctifrons* on a moderately vegetated flood plain near Lawrence, Kansas. The female uses her forelegs in unison for digging, and sand accumulates as a tumulus at the burrow entrance. The nest has an oblique gallery and up to six cells; younger cells are closer to the entrance. Juvenile and adult grasshoppers are used as prey: *Melanoplus differentialis* (Thomas) and *Melanoplus* sp. (Kurczewski also mentioned two museum specimens, one from Beltsville, Maryland, in USNM, pinned with a young female nymph of *Melanoplus* sp., probably *bivittatus* (Say), the other from Polk Co., Minnesota, in UCD, pinned with an adult *Melanoplus infantilis* Scudder). The female carries her prey on the ground, holding it with her mandibles by the antennae (near midlength) and clutching the bases of its midcoxae with her hindlegs; the prey is oriented dorsum up. She enters the nest directly, without releasing her load (the description implies that the nest is permanently open during the provisioning period). One or two prey are stored per cell, venter up and head inward. The egg is laid on the largest prey, on the right or left forecoxal corium, and extends transversely between the fore- and midcoxa.

The males from Saint Anthony Sand Dunes, Idaho (UIM), were collected on flowers of *Helianthus annuus* L.

Geographic Distribution (Fig. 17).—North America between East Coast and Alberta, Idaho, northeastern Utah, and central Texas, north to Massachusetts and southern Alberta, south to Florida and central Texas.

Material Examined.—175♀, 197♂.

Records.—CANADA: **Alberta:** Haynes, 12 km SW Orion, Scandia, Writing-on-Stone Provincial Park. **Manitoba:** Aweme, 3 mi SW Shilo, 2 mi W Stockton. **Saskatchewan:** 10 mi W Moose Jaw.

UNITED STATES: COLORADO: **Bent:** Hasty. **Denver:** Denver. **El Paso:** Colorado Springs. **Jefferson:** 4 mi SW Golden. **Larimer:** Fort Collins. CONNECTICUT: **Hartford:** Windsor. FLORIDA: **Alachua:** Alachua, Gainesville, Monteoca (11 mi NW Gainesville). **Baker:** Glen St. Mary. **Bradford:** —. **De Soto:** Arcadia. **Jefferson:** Monticello. **Lafayette:** Day. **Liberty:** Torreya State Park. **Orange:** Orlando. **Suwannee:** Suwannee River State Park. GEORGIA: **De Kalb:** Stone Mt. **Dougherty:** Albany. **Emanuel:** Swainsboro. **Glynn:** St. Simons Islands. **Lee:** Smithville. **Lowndes:** Valdosta. **McIntosh:** Sapelo Island. **Paulding:** Dallas. **Tift:** Tifton. **White:** Cleveland. IDAHO: **Franklin:** S Weston. **Fremont:** 6 mi NW Saint Anthony, Saint Anthony Sand Dunes. ILLINOIS: Chicago. **Mason:** Sand Ridge State Forest. **McHenry:** Algonquin. IOWA: **Woodsbury:** Sioux City. KANSAS: **Douglas:** Lawrence. MARYLAND: **Prince Georges:** Beltsville. MASSACHUSETTS: **Hampshire:** Southampton. **Worcester:** Holden. MICHIGAN: **St. Joseph:** Constantine. MINNESOTA: **Cass:** —. **Clearwater:** Itasca State Park. **Polk:** —. MISSISSIPPI: **Lafayette:** Oxford. MONTANA: —. NEBRASKA: **Cuming:** West Point. **Hooker:** 1.5 mi N Mullen. **Morrill:** Bridgeport. **Scotts Bluff:** Mitchell. **Sheridan:** Rushville. **Sioux:** Glen, Jim Creek, Monroe Canyon. **Thomas:** Halsey. NEW MEXICO: **De Baca:** Sumner Lake State Park. NEW YORK: **Orange:** West Point. **Suffolk:** Riverhead. NORTH CAROLINA: **Cumberland:** Fort Bragg. **Moore:** Southern Pines. NORTH DAKOTA: **Benson:** Hamar. **McHenry:** Towner. **Ransom:** 3 mi N McLeod, Sheldon. **Ward:** Minot. OKLAHOMA: **Cimarron:** Black Mesa State Park. SOUTH DAKOTA: **Union:** Elk Point. TEXAS: **Lee:** Fedor. UTAH: **Cache:** Cornish, Logan. WISCONSIN: **Milwaukee:** Milwaukee. WYOMING: **Fremont:** Shoshoni.

Tachysphex powelli R. Bohart

(Figure 18)

Tachysphex powelli R. Bohart, 1962:35, ♂, ♀. ! Holotype: ♂, California: Alpine Co.: Winnemucca Lake (CAS).—Krombein 1967:393; Bohart and Menke 1976:276; Krombein 1979:1629.

Diagnosis.—*Tachysphex powelli* has a dull, impunctate mesopleuron (finely rugose in many specimens), the setae are erect on the vertex, erect or nearly so on the mesopleuron, and terga are not fasciate. In the female, the mid- and forefemora are densely punctate (in some specimens also with a few, large punctures basoventrally). In the male, the distance between the clypeal lobe corners is at least equal to the clypeal length, and the forebasitarsus has one to four preapical rake spines. *Tachysphex semirufus* shares these characters, but the setae of the propodeal dorsum are about 1.0 MOD long, erect or nearly so in lateral view. In *powelli*, these setae are about 0.7 MOD long, erect or inclined anterad. Also, the vertex width : length ratio in *powelli* is 1.5–1.7 (female) and 1.6–2.0 (male), while it is 1.1–1.4 (female) and 1.3–1.5 (male) in *semirufus*. The gaster is red in *semirufus*, but it is all black in most *powelli*. Both species occur in cold, sunny habitats, but *powelli* is limited to high altitudes (2,700–3,770 m) of the Sierra Nevada and White Mountains, California, and Ruby Mountains, Nevada, while *semirufus* extends from the Yukon Territory to southern California, and eastward to Ontario, Michigan, and New Jersey (it occurs sympatrically with *powelli* in Sierra Nevada and White Mountains, California).

Description.—Frons punctate or punctatorugose. Vertex and scutum with well-defined punctures, vertex punctures less than one diameter apart. Mesopleuron finely rugose to (some specimens) microareolate. Propodeal dorsum ridged or rugose, at least basally; side rugose, irregularly ridged, or (some specimens) microareolate; hindface usually ridged, but ridges evanescent in some individuals. Sternum I without apical depression. Discal micropuncture of tergum II one to two diameters apart. Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit. Setae erect, their length (in MOD): one on vertex and mesopleuron, about 0.5 on scutum; about 0.7 on propodeal dorsum; setae of midfemoral venter appressed, or erect in apical half, about 0.3 MOD long.

Head, thorax, and gaster black, or gaster partly red (see Variation below). Legs black, tarsal apex brown. Terga not fasciate.

FIGURE 17. Geographic distribution of *Tachysphex punctifrons* W. Fox.

FIGURE 18. Geographic distribution of *Tachysphex powelli* R. Bohart.

Wings strongly infumate in female, weakly to strongly so in male.

♀.—Clypeus: bevel shorter to longer than basomedian area; lip arcuate, entire or (some specimens) shallowly emarginate mesally and incised laterally. Dorsal length of flagellomere I 2.0–2.4× apical width. Vertex width 1.5–1.7× length. Scutal punctures less than one diameter apart or most discal punctures two to three diameters apart. Tergum V densely to sparsely punctate (punctures evanescent in some specimens), its apical depression impunctate. Pygidial plate shiny, punctate. Trochanteral and femoral punctation dense. Length 7.5–11.0 mm.

♂.—Mandibular inner margin with tooth. Clypeus: bevel shorter than basomedian area; lip arcuate or truncate, its corners rectangular to obtuse, separated by a distance equal to 1.1–1.4 of clypeal length and to 1.0–1.3 of distance between a corner and orbit. Dorsal length of flagellomere I 1.1–1.3× apical width. Vertex width 1.6–2.0× length. Scutal punctures subcontiguous or (some specimens) many discal punctures one to two diameters apart. Sterna densely punctate. Forefemoral notch glabrous, margined posteriorly in many specimens. Forebasitarsus with one to three preapical rake spines; outer apical spine of foretarsomere II longer than tarsomere width. Length 6.5–9.0 mm.

VARIATION.—The gaster is all black in most specimens, but it is partly red in some individuals. Of the two females from Blue Canyon near Sonora Pass collected on 10 August 1960 by J. W. MacSwain (CAS), one is all black and the other has terga I–III and a large part of sternum II dark red. Otherwise these two individuals are identical. Most females from Sonora Pass are all black, but one female examined (UCD) has largely red terga I–III. Unlike other males examined, the holotype of *powelli* has a reddish dark apicomedian zone on tergum II.

GEOGRAPHIC DISTRIBUTION (Fig. 18).—Sierra Nevada and White Mountains in California, and also Ruby Mountains in Nevada, at the elevation 2,700–3,770 m (7,800–12,400 ft).

MATERIAL EXAMINED.—53♀, 62♂ (CAS, CIS, CSDA, SDNH, TLG, UCD, USNM).

RECORDS.—UNITED STATES: CALIFORNIA: **Alpine:** Ebbetts Pass, Winnemucca Lake. **El Dorado:** Strawberry Lake. **Fresno:** Heart Lake, Horseshoe Lakes, Humphreys Basin (14 mi SW Bishop), Nellie Lake (R. Bohart 1962), Pioneer Basin (10–11,000 ft). **Inyo:** Campito Mountain (White Mts.), Mono Pass, Rock Creek Lakes (9,700 ft), Ruby Lake. **Mono:** Mammoth Lake, Sonora Pass, 1 mi W Tom's Place, White Mts. (9 air mi N Inyo Co. line, Patriarch Grove, Sheep Mt.). **Nevada:** Mt. Lola (8 mi NE Soda Springs). **Tulare:** Kings Canyon National Park (Muir Trail 12,300 ft, above Lake 12,248 ft—headwaters of Bubbs Creek), Mineral King, Mosquito Lakes, Sequoia National Park (Muir Trail 2–3 mi S Forester Pass, 1.5 mi S Lake South America, Tyndall Creek). **Tuolumne:** Sonora Pass, Sonora Peak, Tioga Pass, Tuolumne Meadows, Upper Gaylor Lake near Tioga Pass. NEVADA: **Elko:** below Liberty Lake in Ruby Mts. (1♂, CAS).

Tachysphex semirufus (Cresson)

(Figures 19, 20)

Larrada semirufa Cresson, 1865:464, ♀. ! Lectotype: ♀, Colorado: no specific locality (ANSP), designated by Cresson 1916:96.—Riley 1878:317.—In *Larra:* Patton 1881:389, Ashmead 1890:33.—In *Tachysphex:* Ashmead 1894:63; W. Fox 1894*a*:515; Dalla Torre 1897:685, Ashmead 1899:25; Rohwer 1911:580 (in key), Mickel 1918:422, G. Bohart 1951:952, Krombein 1967:393; Bohart and Menke 1976:276, Krombein 1979:1629; Kurczewski and Evans, 1986:721.

Tachysphex punctulatus H. Smith, 1906:246, ♀. ! Holotype: ♀, Nebraska: Sioux Co.: no specific locality (UNL). Nec Kohl, 1884. Synonymized by G. Bohart 1951:952.—Rohwer 1911:580 (in key)

Tachysphex puncticeps H. Smith, 1908:381 (new name for *Tachysphex punctulatus* H. Smith, 1906, nec Kohl, 1884). Nec Cameron, 1903. Synonymized by G. Bohart 1951:952.—Mickel 1918:424

Tachysphex giffardi Rohwer, 1917*b*:244. ! Holotype: ♀, California: Placer Co.: Summit (USNM). Synonymized by G. Bohart 1951:952

DIAGNOSIS.—*Tachysphex semirufus* has a dull, uniformly microareolate mesopleuron (Fig. 19b); nonfasciate terga; setae 1.0 MOD long and erect on the vertex and propodeal dorsum in

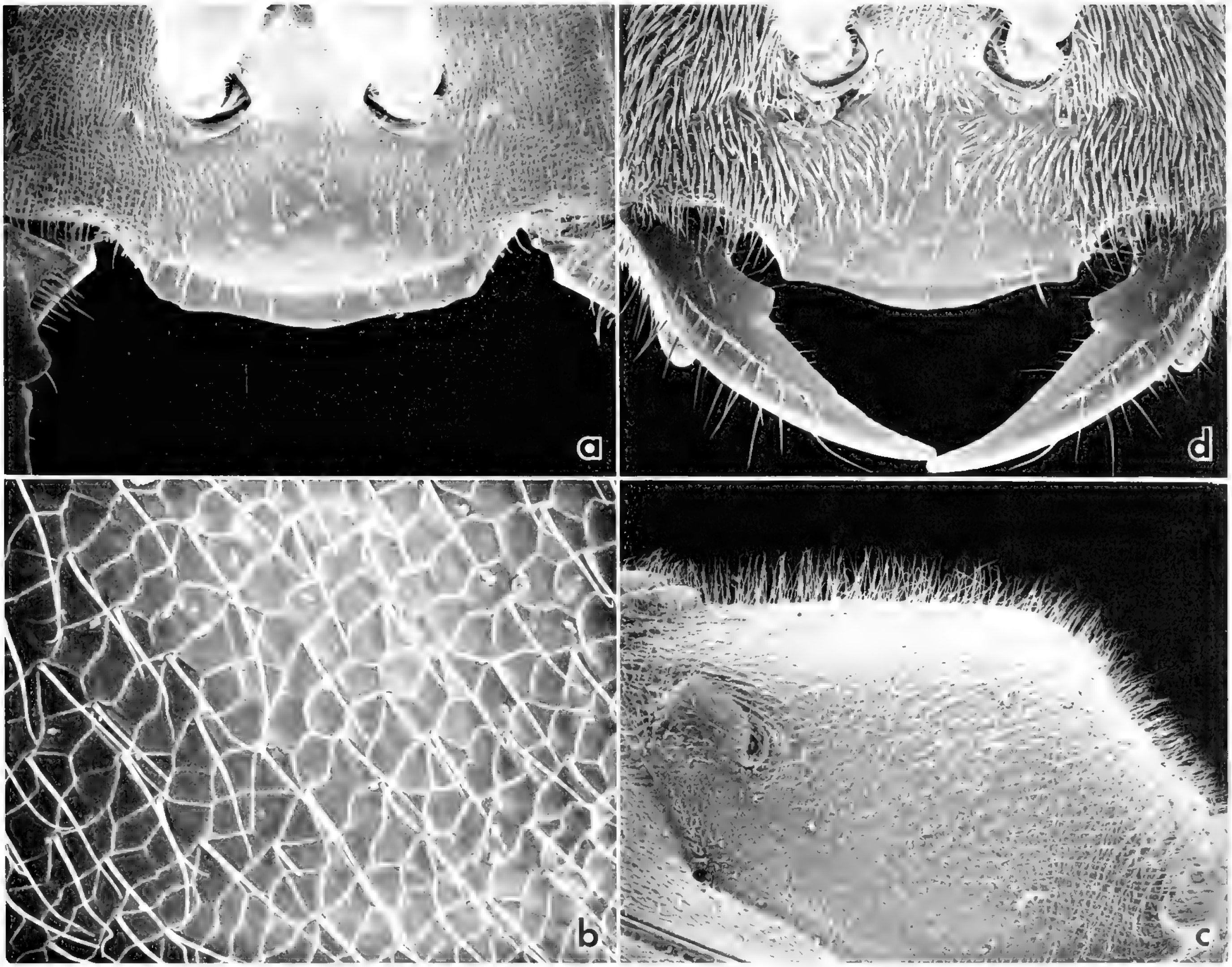

FIGURE 19. *Tachysphex semirufus* (Cresson): a—female clypeus; b—mesopleural sculpture of female; c—female propodeum, lateral view; d—male clypeus

lateral view (Fig. 19c), 1.0 MOD long and erect or slightly inclined on the mesopleuron; and the male forebasitarsus with three or four preapical rake spines. *Tachysphex powelli* and *tahoe* are similar (see these species for differences). *Tachysphex mirandus* is also similar, but *semirufus* differs in having the femoral venter densely micropunctate, the mesothoracic venter densely punctate, the male clypeal lobe nontriangular, and the male mandible with a tooth on the inner margin (Fig. 19d). In *mirandus*, the female fore- and midfemur basoventrally have sparse punctures but no micropunctation (Fig. 71b), the male clypeal lobe is triangular, the inner mandibular margin is not dentate (Fig. 71c), and the mesothoracic venter of most specimens (both sexes) is sparsely punctate.

DESCRIPTION.—Frons dull, its punctures shallow, in most specimens less than one diameter apart. Vertex punctures more than one diameter apart, but less than that in some males. Mesopleuron dull, impunctate, evenly microareolate (Fig. 19b). Propodeal dorsum evenly microareolate; side microareolate or microridged; hindface ridged or uniformly microsculptured (especially in males). Sternum I without apical depression. Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit. Setae erect or suberect, 1.0 MOD long on vertex, mesopleuron, and propodeal dorsum (Fig. 19c); 0.3–0.5 MOD long on scutum, at middle inclined evenly posterad. Apical half of midfemoral venter with erect or suberect setae that are 0.5–1.0 MOD long.

Head, thorax, and legs black, tarsal apex reddish. Gaster usually red, but terga III–VI black in a female from Glendo, Wyoming, and terga I and IV–VII black in some males from British Columbia and Saskatchewan. Terga not fasciate. Wings infumate, often with violet reflection, but almost hyaline in many males. Frontal vestiture silvery.

♀.– Clypeus (Fig. 19a): bevel much longer than basomedian area; lip arcuate, not emarginate, usually with short, obtuse projection mesally, incised laterally in some specimens. Dorsal length of flagellomere I 2.4–3.0× apical width. Vertex width 1.1–1.4× length. Scutal punctures subcontiguous to many di-

ameters apart at middle (usually two to three diameters apart). Tergal microsculpture fine, variably developed, sometimes almost absent (and then the integument is highly polished); micropuntures of tergum II two or three to many diameters apart. Tergum V impunctate or with a few, sparse punctures; its apical depression impunctate. Pygidial plate smooth or alutaceous, punctate. Trochanteral punctures minute, dense to sparse on venter. Punctures of forefemoral venter minute, usually sparse basally. Length 6–11 mm.

♂.—Mandibular inner margin with tooth (Fig. 19d). Clypeus (Fig. 19d): bevel indistinctly delimited posteriorly, about as long as basomedian area; lip evenly arcuate, its corners obtuse, closer to orbit than to each other; a small, longitudinal carina extends from each lip corner. Dorsal length of flagellomere I 1.3–1.8 × apical width. Vertex width 1.3–1.5 × length. Scutal punctures subcontiguous. Micropunctures of tergum II two to three diameters apart at middle. Sternal punctures fine, dense, except for impunctate apical depression of sterna II–V. Forefemoral notch glabrous. Foretarsus with three or four preapical rake spines; outer apical spine of foretarsomere II equal to tarsomere III or longer. Length 5–6 mm.

Life History.—Riley (1878) reported that *semirufus* preyed on young nymphs of the Rocky Mountain grasshopper, *Melanoplus spretus* (Walsh), but his identification of the wasp is not certain. Krombein (1967) also lists immature *Melanoplus* as prey of this species, but his information is probably based on Riley (1878). H. Smith's (1908) record of *semirufus* visiting flowers of *Astragalus* is also questionable. Kurczewski and Evans (1986) described the provisioning behavior of a female in Jackson Hole, Wyoming: the wasp proceeded forward on the ground, holding her prey with the mandibles by the base of its antennae. She entered an open nest, deposited the prey, and started closing the burrow using material from the tumulus. The burrow entered the soil obliquely and ended in a single cell that contained a single prey, a nymphal mormon cricket *Anabrus simplex* Haldemann (Tettigoniidae). A female of *semirufus* from Santa Clara, Utah (USU) is pinned with her prey, also a young tettigoniid, a *Capnobates* sp., probably *occidentalis* (Thomas), det. D. C. F. Rentz.

Geographic Distribution (Fig. 20).—Montane areas between Yukon Territory, southern California and Arizona, east to Colorado and western Nebraska; also southern Ontario, New Jersey, and Michigan.

Material Examined.—290♀, 63♂.

Records.—CANADA: **Alberta:** 5 mi W Smith, Wamamun. **British Columbia:** Blueberry, Nicola, Osoyoos. **Ontario:** Constance Bay, Merivale near Ottawa. **Saskatchewan:** Great Sand Hills, Landing, Rosthern. **Yukon Territory:** Whitehorse.

UNITED STATES: ARIZONA: **Cochise:** Huachuca Mts. **Coconino:** Grand Canyon National Park. CALIFORNIA: **Alameda:** Tesla Road. **Alpine. Amador:** Fiddletown. **El Dorado. Fresno:** 3 mi E Redinger Lake. **Glenn:** Black Butte, Plaskett Meadows. **Inyo:** Mono Pass (ca. 10 mi S Tom's Place, near county line). **Kern:** Walker Pass. **Kings:** 6 mi SW Avenal. **Lassen:** Doyle, Susanville. **Los Angeles:** Bell Canyon, Little Rock, Pasadena, San Gabriel Canyon, 6 mi NE Three Points. **Modoc. Mono:** McGee Creek (8 mi W Tom's Place), Sardine Creek, White Mts. (Blanco's Corral, Crooked Creek). **Monterey:** Chews Ridge near White Oak Camp, Pacific Grove. **Napa:** 6 mi W Oakville. **Nevada:** Donner Lake, Prosser Dam, Sagehen Creek near Hobart Mills. **Placer:** Carnelian Bay on Lake Tahoe, Summit. **Plumas:** Bucks Lake, 10 mi S Johnsville. **Riverside:** Lake Fulmor. **San Bernardino:** 4 mi NW Crestline, 5 mi N Vidal Junction. **San Diego:** Borrego, Julian, Lake Wohlford, Potrero. **San Luis Obispo:** Cuyama Valley. **Santa Barbara:** New Cuyama (also 10 mi W). **Shasta:** Lassen Peak trail, 3 mi SE Mt. Lassen. **Sierra:** Packer Creek. **Siskiyou:** Dry Lake Lookout (7 mi NNW town of Klamath River), Mt. Shasta (6,000 ft), Walker. **Trinity:** Buttercreek Meadow, Covington Mill, Hayfork Bally. **Tulare:** Bear Creek (5 mi NE Springville), Quaking Aspen, Sequoia National Park. **Tuolumne. Ventura:** Mt. Pinos (7,500–8,800 ft). **Yolo:** Rumsey. COLORADO: **Alamosa:** Great Sand Dunes National Monument. **Boulder:** Nederland. **Clear Creek:** Mount Evans (elev. 11,600 ft). **Costilla:** Ute Creek. **Denver:** Denver. **Gunnison:** 3 mi N Gothic. **Jackson:** Walden. **Jefferson:** Platte Canyon. **Larimer:** Camp Creek Ranger Station (about 41°0'N, 106°12'W), Fort Collins. IDAHO: **Bear Lake:** Bloomington Lake. **Clearwater:** Beaver Ridge. **Gooding:** 5 mi N Bliss. **Lemhi:** Bannock Pass, Meadow Lake (6 mi W Gilmore). **Lincoln:** Dietrich Butte, Owynza. **Minidoka:** Minidoka. **Twin Falls:** Rock Creek Canyon. MICHIGAN: **Alger:** Pictured Rocks National Lakeshore. **Benzie:** Sleeping Bear Dunes. **Clare:** —. **Livingston:** E. S. George Reserve. **Marquette:** Huron Mountain Club. **Osceola:** Tustin. NEBRASKA: **Sioux:** Monroe Canyon. NEVADA: **Clark:** Boulder Dam. **Elko:** Harrison Pass, Lamoille Canyon (Ruby Mts.). **Humboldt:** Winnemucca. **Lander:** Kingston Canyon. **Pershing:** 40 mi NW Lovelock. **Washoe:** Galena Creek, Incline Village, Mt. Rose, Steamboat. NEW JERSEY: **Burlington:** Browns Mills Junction (1♀, UCD). **Camden:** Clementon (1♀, UCD). OREGON: **Clackamas:** Mt. Hood (timberline near Government's Camp). **Klamath:** Aspen Lake, Eagle Ridge on Klamath Lake, Klamath Falls, Sun Pass. **Lake:** Abert Lake. UTAH: **Box Elder:** Promontory Point. **Cache:** Cache National Forest, Tony Grove. **Millard:** 8 mi W Hatton. **Washington:** Santa Clara. **Weber:** Willard Peak. WASHINGTON: **Benton:** 2 mi W Wallula Junction. **Walla Walla:** McNary Natural Wildlife Refuge. WYOMING: **Fremont:** Chimney Rock Peak (Wind River Range). **Hot Springs:** Thermopolis. **Laramie:** Cheyenne. **Lincoln:** Kemmerer. **Platte:** Glendo, Guernsey. **Sweetwater:** Green River. **Teton.**

Tachysphex pauxillus W. Fox

(Figures 21, 22)

Tachysphex pauxillus W. Fox, 1894*a*:530, ♀. ! Holotype: ♀, California: no specific locality (ANSP).—Dalla Torre 1897:683; Ashmead 1899:250; Cresson 1928: 45; G. Bohart 1951:951; Bohart and Menke 1976:275; Krombein 1979:1629; Rust et al. 1985:46, Kurczewski and Evans 1986:720.

Tachysphex nigrior W. Fox, 1894*a*:530, ♀, ♂. ! Lectotype: ♀, State of Washington: no specific locality (ANSP), designated by Cresson 1928:45. Synonymized by Pulawski *in* Krombein 1979:1629.—Dalla Torre 1897:681; Ashmead 1899:250; G. Bohart 1951:951; Krombein 1967:393; Evans 1970:490, 497; Bohart and Menke 1976:275.

Diagnosis.—*Tachysphex pauxillus* has a distinctive mesothoracic sculpture (Fig. 21c): the mesopleuron is alutaceous, with inconspicuous vestiture and minute punctures that are one (some males) to many diameters apart. In addition, many punctures of the scutal disk are more than one diameter apart in nearly all females and most males. The thick gena in dorsal view (Fig. 21b, e) is a subsidiary recognition character.

Description.—Frons strongly microsculptured, finely punctate, most punctures less than one diameter apart or (some specimens) more than one diameter apart. Vertex alutaceous, finely punctate, punctures at middle less than one to several diameters apart. Mesopleuron alutaceous, finely punctate (Fig. 21c). Propodeal dorsum irregularly rugose or evenly microareolate; side and hindface ridged (ridges evanescent in some specimens). Sternum I without apical depression. Hindcoxa not carinate.

Frontal vestiture weak, integument easily visible between antennal socket and orbit. Midscutal setae oriented posterad. Midfemoral venter almost glabrous.

Body black or gastral terga I–III and sternum II red (all black males are more common than all black females); tarsal apex brownish. Terga not fasciate or terga II and III of some males with inconspicuous, silvery fascia. Frontal vestiture silvery. Wings infumate, only weakly so in some males.

♀.—Clypeus (Fig. 21a): bevel much longer to a little shorter than basomedian area; lip almost straight, in most specimens shallowly incised laterally. Dorsal length of flagellomere I 1.4–2.0 × apical width. Vertex width 1.6–1.8 × length. Scutum shiny (except anteriorly), its punctures fine, averaging several diam-

FIGURE 20. Geographic distribution of *Tachysphex semirufus* (Cresson)

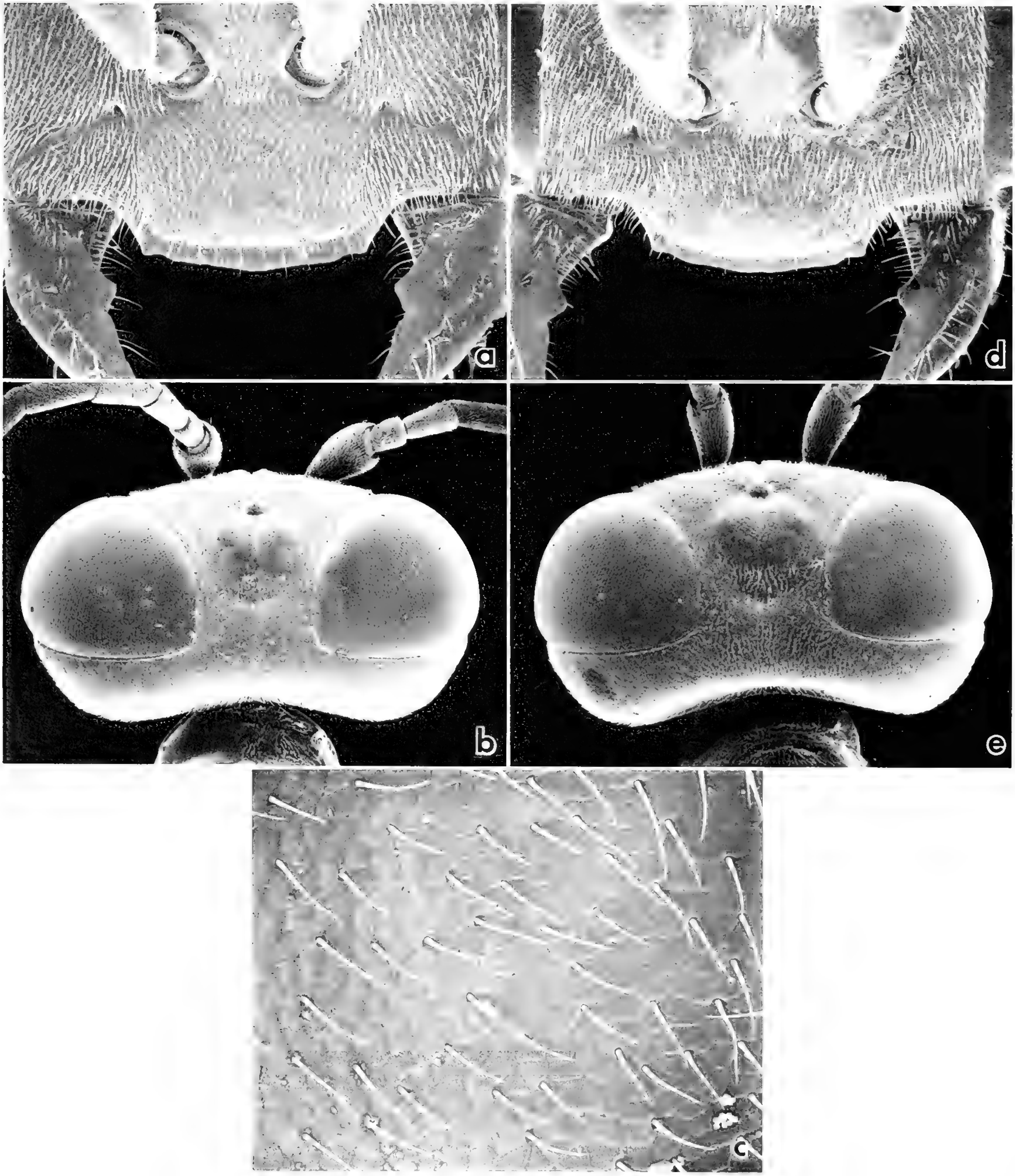

FIGURE 21. *Tachysphex pauxillus* W. Fox. a—female clypeus; b—female head from above; c—mesopleural sculpture of female; d—male clypeus; e—male head from above.

eters apart, but less than one diameter apart in some specimens. Mesopleural punctures inconspicuous, evanescent in some individuals, two to several diameters apart. Micropunctures of tergum I (except basally) and II several diameters apart. Tergum V sparsely punctate. Trochanteral punctures mostly dense, but sparse on venter in some specimens. Forefemoral venter alutaceous, finely punctate (punctures sparse, at least at middle). Length 6–9 mm.

Vertex setae erect, 1.0 MOD long anteriorly, subappressed posteriorly. Scutal setae sparse, erect or suberect, slightly shorter than MOD.

♂.—Mandibular inner margin with tooth (Fig. 21d). Clypeus (Fig. 21d): bevel about as long as basomedian area; lip weakly arcuate, its corners obtuse, closer to orbits than to each other. Dorsal length of flagellomere I 0.9–1.1× apical width. Vertex width 1.8–2.2× length. Scutum shiny, finely punctate, discal punctures often averaging more than one diameter apart. Mesopleural punctures shallow, in most specimens inconspicuous, one to many diameters apart. Discal micropunctures of tergum II two to four diameters apart. Sterna densely punctate throughout. Forefemoral notch pruinose. Foretarsus without rake; outer apical spine of tarsomere II much shorter than III. Length 5–8 mm.

Vertex setae erect at least anteriorly, 0.5–0.7 MOD long. Scutal setae suberect, about 0.5 MOD long.

Life History.—Two females examined (USU) were collected on flowers of *Daucus carota* L. in Logan, Utah. Evans (1970, as *nigrior*) observed a female transporting her prey, a grasshopper, which she was holding by the antennae with her mandibles. Her nest was open and had a small mound of sand at the entrance. Before leaving, she closed the entrance. The shallow cell contained one prey, with egg laid transversely behind the front coxae. The grasshopper was an immature *Melanoplus* sp., about the same size as the wasp.

Evans (1970) found two males of *pauxillus* among the prey of *Philanthus pulcher* Dalla Torre.

Geographic Distribution (Fig. 22).—Montane areas between southern British Columbia and southern California, east to Colorado and Nebraska (unknown from the Great Basin area).

Material Examined.—214♀, 155♂.

Records (b: gaster all or predominantly black; r: gaster red basally).—CANADA: **British Columbia:** Richter Pass Road 8 mi W Osoyoos (b).

UNITED STATES: CALIFORNIA: **Alameda:** 1 mi E Mission Peak (b, r). **Contra Costa:** Castle Rock (b), Mt. Diablo (b, r), Las Trampas Ridge W Danville (b). **El Dorado:** Bijou (b), Blodgett Forest 13 mi E Georgetown (r), Fallen Leaf Lake (b), 8 mi N on Ice House Road (b), Meyers (b). **Fresno:** Mendota (r), Panoche Road (r). **Glenn:** Artois (b). **Lake:** Middleton (r). **Lassen:** Norvell (r). **Marin:** Olema (r), Mt. Tamalpais State Park (b, r). **Mendocino:** Hopland Field Station (b, r), Inglenook Fen 0.5 mi N Fort Bragg (b, r). **Modoc:** 8 mi N Adin (r), 6 mi NW Cedarville (b). **Mono:** White Mts., Patriarch Grove (r). **Monterey:** Bryson (r). **Napa:** Angwin (r). **Nevada:** Independence Lake (b), Sagehen Creek near Hobart Mills (b, r). **Placer:** Baxter (b), Carnelian Bay on Lake Tahoe (b, r), Dutch Flat (b, r), 4 mi S Rocklin (r). **Plumas:** Buck's Lake (b, r), Johnsville (b). **Riverside:** Herkey Creek in San Jacinto Mts. (r). **Sacramento:** Sacramento (r). **San Diego:** Alpine (b). **San Francisco:** Presidio Park (b, r). **San Mateo:** Menlo Park (b, r). **Santa Barbara:** Santa Cruz Island (Christi Beach: r; Prisoner's Harbor: r), Santa Rosa Island (Beechers Bay: r; Windmill Canyon North Fork: b, r). **Shasta:** Shingletown (b). **Sierra:** Independence Lake (b, r), Sierra Valley (b), Sierraville (r), Yuba Pass (b, r). **Siskiyou:** Dry Lake Mountain 7 mi NNW town of Klamath River (b, r). **Stanislaus:** 3.2 mi W Highway 120 on Evergreen road (r). **Trinity:** Hayfork (r), Scott Mt. (r). **Tuolumne:** Dodge Ridge Ski Area (b), Mather (b, r). **Yolo:** Davis (r). COLORADO: **Clear Creek:** Mt. Evans, 12,000 ft (b). **Larimer:** Tundra Curves in Rocky Mountains National Park. IDAHO: **Bear Lake:** Georgetown (b). **Boise:** 1

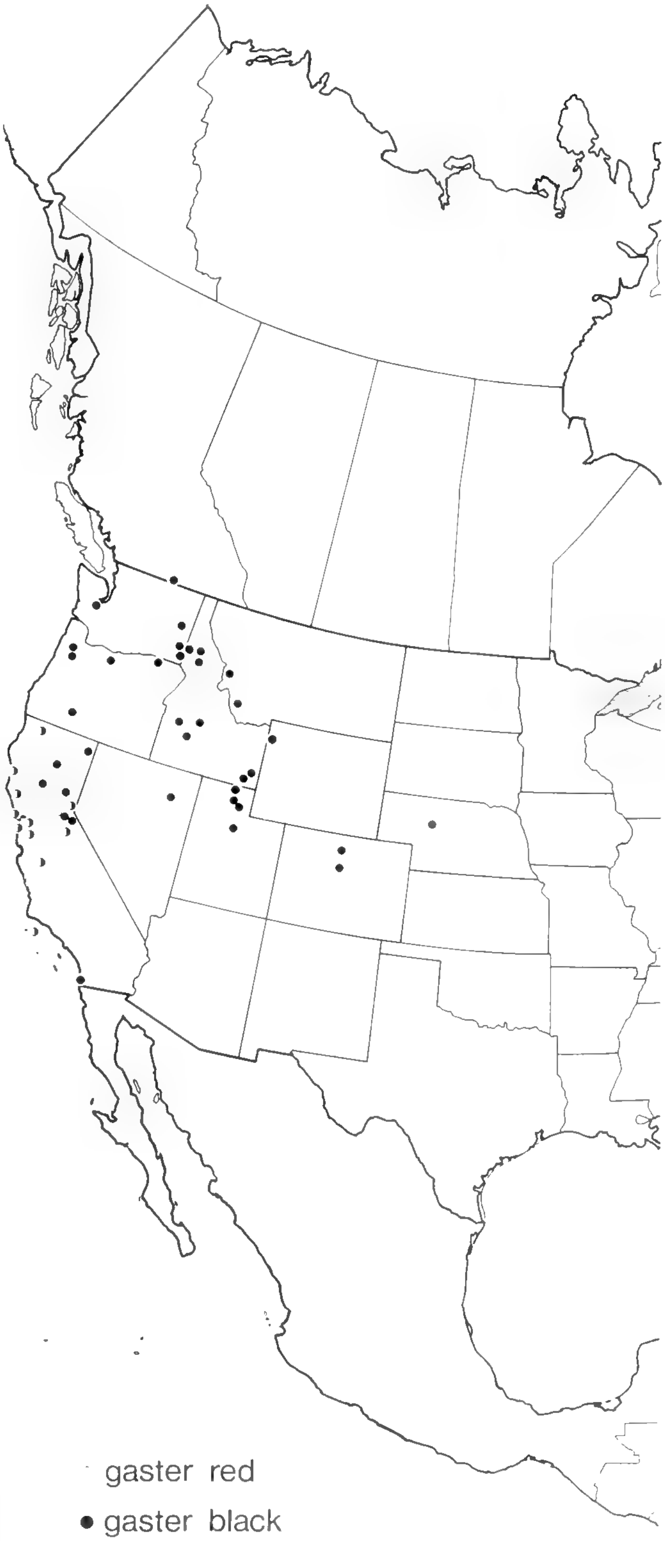

Figure 22. Geographic distribution of *Tachysphex pauxillus* W. Fox.

mi W Horseshoe Bend (b). **Clearwater:** Elk River (b), 10 mi N Nez Perce (b). **Custer:** Sawtooth Lake (b). **Elmore:** Dixie (b). **Franklin:** Cub River Canyon (b), Minkcreek (b). **Latah:** 4 mi N Moscow (also 7 mi NE, b), Moscow Mt. (b), Upper Palouse River (b). MONTANA: **Beaverhead:** 3 mi W Jackson (b). **Ravalli:** Ham-

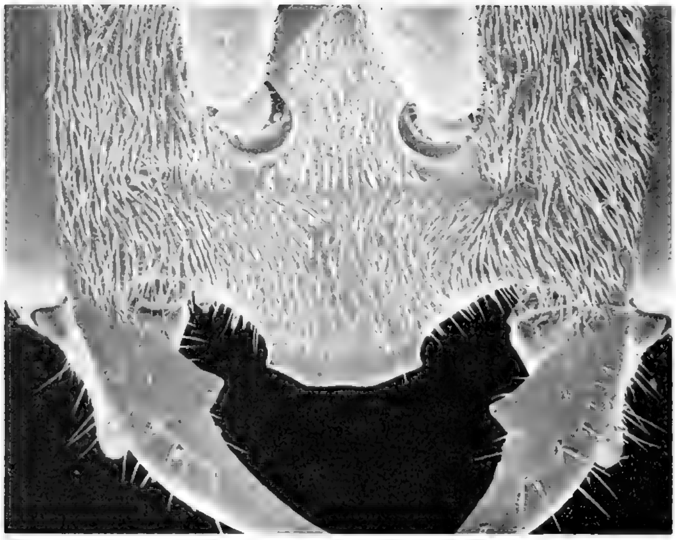

FIGURE 23. *Tachysphex eldoradensis* Rohwer: a—male clypeus.

ilton (b). NEBRASKA: **Hooker:** 1.5 mi N Mullen (b). NEVADA: **Elko:** Ruby Mts (b) (Favre Lake, Island Lake, Lamoille Canyon, Liberty Lake). OREGON: **Benton:** Adair (b). **Klamath:** Upper Klamath Marsh (b). **Marion:** Salem (b). **Umatilla:** Milton–Freewater (b). **Wasco:** 5 mi S Dufur (b). UTAH: **Cache:** Airport (b), Benson Ward (b), Blacksmith Fork (b), High Creek (b), Logan (b), Logan Canyon (b), Newton (b), River Heights (b), Sardine Canyon (b), Wellsville (b), Willard Peak (b). **Utah:** Provo (b). **Weber:** Ogden (b). WASHINGTON: **Asotin:** Asotin (b). **Spokane:** Medical Lake (b), Tyler (b). **Thurston:** Olympia (b). **Walla Walla:** Mill Creek (b). **Whitman:** Almota (b), Pullman (b). WYOMING: **Teton:** Pilgrim Creek in Teton National Forest (b), Moran (b)

Tachysphex eldoradensis Rohwer

(Figures 23, 24)

Tachysphex eldoradensis Rohwer, 1917*b*:245, ♀, ! Holotype: ♀, California: El Dorado Co.: Tahoe (USNM).—G. Bohart 1951:951; Krombein 1967:393; Bohart and Menke 1976:273, Krombein 1979:1628

DIAGNOSIS.—*Tachysphex eldoradensis* has a dull, indistinctly punctate mesopleuron (weakly rugose in some individuals). The female can be recognized by its shiny, sparsely punctate trochanteral venter, its broad vertex (vertex width 1.4–1.9 × length), and by its large size (body length 9.0–10.5 mm). Several other species (*aethiops, crenulatus, irregularis, musciventris,* and *orestes*) also have a sparsely punctate trochanteral venter, but they have unique characters that are absent in *eldoradensis* (see these species for details).

Males of *eldoradensis* have an unusually narrow but prominent clypeal lobe (Fig. 23): the lip corners are much closer to each other than to orbit and the distance between the corners equals 0.45–0.7 of clypeal length. In addition, the foretarsal rake is well developed, and the propodeal side is not ridged. Males of *hopi* are similar, but in *eladoradensis* punctures are finer on sterna than on the mesothoracic venter and extend to the sternal hindmargin, and in most specimens the trochanteral venter is impunctate or sparsely punctate. In *hopi*, punctures are slightly coarser on the sterna than on the mesothoracic venter, sterna II–IV of most specimens have a narrow impunctate zone apically (or only apicolaterally), and the trochanters are densely, finely punctate. Altitudinal distribution also helps identification: *eldoradensis* occurs between 900 m (e.g., in Siskiyou County, California) and 3,300 m in the White Mountains, California, while *hopi* is a low elevation species (almost sea level in Marin County, California to 1,800 m near Strawberry, Tuolumne County, California). Because of its narrow clypeal lobe, the male of *eldoradensis* can also be confused with *occidentalis* and *bohartorum.* However, its clypeal lip is angulate, and the mandibular inner margin has a tooth (in *occidentalis,* the clypeal lip is rounded laterally, and the mandibular inner margin is not dentate). Males of *bohartorum* have a distinctive gastral punctation (see that species for details).

DESCRIPTION.—Punctures less than one diameter apart on frons, vertex, and scutum. Mesopleuron dull, densely, shallowly, indistinctly punctate, weakly rugose in some specimens. Propodeal dorsum evenly microreticulate, side at most (in large females) with vestigial ridges; hindface ridged, only weakly so in some individuals. Discal micropunctures of tergum II two to three diameters apart. Sternum I without apical depression. Hindcoxa not carinate.

Vestiture almost totally hiding integument between antennal socket and orbit. Scutal and femoral setae appressed.

Head, thorax, and legs black, tarsal apex reddish. Gaster red (only three basal segments in specimens from British Columbia and Montana, the remainder being black). Wings moderately infumate. Frontal vestiture silvery.

♀.—Clypeus: bevel shorter to longer than basomedian area; lip weakly arcuate, with one shallow, lateral incision on each side, in some specimens also with vestigial, mesal notch. Dorsal length of flagellomere I 2.1–2.4 × apical width. Vertex width 1.4–1.9 × length. Tergum V densely punctate, but apical depression impunctate in some specimens. Pygidial plate alutaceous, punctate. Trochanteral venter shiny, with few, sparse punctures. Punctures of femoral venter fine, dense, but in some individuals basally sparse. Length 9.0–10.5 mm.

Postocellar impression with erect setae whose length is almost 1.0 MOD.

Terga I–IV at most weakly silvery fasciate apically (fasciae inconspicuous or absent).

♂.—Mandibular inner margin with tooth (Fig. 23). Clypeus (Fig. 23): bevel indistinctly delimited posteriorly, shorter to longer than basomedian area; lip arcuate, with obtuse corners; distance between corners equal to 0.6–0.7 of clypeal length and also of distance between corner and orbit. Dorsal length of flagellomere I 1.0–1.3 × apical width. Vertex width 1.6–1.7 × length. Sterna densely punctate throughout, punctures finer than on mesothoracic venter. Trochanteral venter shiny, sparsely punctate (most specimens), or with dense punctures (e.g., in a male from Dodge Ridge Ski Area, California, whose sternal punctures are as in remaining *eldoradensis*). Forefemoral notch marginate, glabrous. Forebasitarsus with three or four preapical rake spines; outer apical spine of foretarsomere II as long as foretarsomere III or longer. Length 6–8 mm.

Vertex setae erect, as long as MOD on postocellar impression.

Terga I–III silvery fasciate apically (certain specimens) or fasciae absent.

GEOGRAPHIC DISTRIBUTION (Fig. 24).—California (mainly Sierra Nevada) to Washington and Montana, east to Wyoming and Colorado.

MATERIAL EXAMINED.—56♀, 67♂ (CAS, CIS, CSDA, CSU, KU, NSDA, NYSU, UCD, UIM, USNM, USU, WJP, WSU)

RECORDS.—UNITED STATES: CALIFORNIA: **Alpine:** Hope Valley, Winnemucca Lake. **El Dorado:** Desolation Valley Primitive Area, Meyers, Tahoe. **Lassen:** Bridge Creek Camp, Summit Camp. **Mariposa:** Lake Tenaya. **Mendocino:** 2.5 air mi N Eel River Ranger Station. **Modoc:** 3 mi E Willow Ranch. **Mono:** Sonora

Pass, Tioga Lake, White Mts. (Blanco's Corral, 10,000 ft, Crooked Creek). **Nevada:** Boca, Sagehen Creek near Hobart Mills. **Shasta:** Lassen Volcanic National Park. **Sierra:** Sardine Creek (ca. 1 mi NW Bassetts). **Siskiyou:** 27 road mi NE Weed. **Tuolumne:** Dodge Ridge Ski Area near Strawberry. COLORADO: **Grand:** Troublesome. **Mineral:** Creede. IDAHO: **Bear Lake:** 5 mi W Ovid. **Custer:** Challis. **Fremont:** 6 mi NW St. Anthony, St. Anthony Sand Dunes. **Lincoln:** Kimama, Owinza, Shoshone. **Oneida:** 5 mi NW Holbrook. MONTANA: **Gallatin:** Three Forks. NEVADA: **Elko:** 6 mi S Deeth, Lamoille Canyon. **Humboldt:** Santa Rosa Range. **Pershing:** Lovelock, 7 and 13 mi E Oreana. **Washoe:** Mt. Rose. **County unknown:** Wells. OREGON: **Baker:** Baker, Unity. **Grant:** Dixie Butte Spring. **Harney:** Antelope Mt. in Steens Mts. **Klamath:** Lake of the Woods. **Morrow:** Boardman. **Umatilla:** Hermiston. UTAH: **Cache:** Franklin Basin, Logan Canyon. WASHINGTON: **Yakima:** Toppenish. WYOMING: **Carbon:** Medicine Bow. **Fremont:** Horse Creek Camp (12 mi N Dubois), South Pass. **Sweetwater:** Green River. **Teton:** Jenny Lake, 14 km SW Moran Post Office

Tachysphex hopi sp. n.

(Figures 25, 26)

Derivation of Name.—Named after the Hopi Indians of Arizona; a noun in apposition.

Diagnosis.—Females of *hopi* have an apicomedian process of varying size on the forecoxa (Fig. 25b, c), and slender, elongate tarsomeres IV and V (Fig. 25d, e). This combination of characters distinguishes *hopi* from other species except *bohartorum* and most *occidentalis*. The laterally incised clypeal lip (Fig. 25a) and black femora distinguish *hopi* from *occidentalis* (in which the clypeal lip is entire and the hindfemur is red). The frontal vestiture of *hopi* is silvery (golden in *bohartorum*) and the lateral incision of the clypeal bevel is shallow (deep in *bohartorum*). The apicoventral margin of tarsomere V is concave in *hopi*, slightly less so in *bohartorum*, and straight or nearly so in other species of the *pompiliformis* group.

The male of *hopi* is very similar to *eldoradensis*. See that species for differences (p. 46).

Description.—Punctures subcontiguous on frons, vertex, mesothorax, trochanters, and femora. Mesopleuron dull, microsculptured, its punctures shallow, ill defined. Propodeum microareolate or hindface finely ridged. Sternum II without apical depression. Hindcoxa not carinate.

Integument hidden (or nearly so) by vestiture between antennal socket and orbit. Setae: appressed on mesothorax and femora except subappressed on hypoepimeral area; on vertex erect, about 1.0 MOD long (less than MOD posteriorly); on scutum at middle oriented posterad; on propodeal dorsum mesally nearly appressed, oriented anterolaterad.

Head, thorax, and legs black, tarsal apex reddish. Gaster red in most specimens, but segments IV–VI black in females from Alberta, and segments IV–VII darkened in some males. Terga I–III silvery fasciate apically (fasciae inconspicuous). Wings slightly infumate. Frontal vestiture silvery.

♀.—Clypeus (Fig. 25a): bevel shorter than to longer than basomedian area; lip free margin arcuate to nearly straight mesally, not emarginate mesally, shallowly incised laterally. Dorsal length of flagellomere I 2.1–2.2 × apical diameter. Vertex width 1.4–1.5 × length. Discal punctures of tergum II up to several diameters apart. Tergum V with impunctate apical depression. Pygidial plate punctate, alutaceous to unsculptured between punctures. Forecoxa with apicomedian process of varying size (Fig. 25b, c). Hindtarsomeres IV and V slenderer than average in the *pompiliformis* group (Fig. 25d, e), hindtarsomere IV emarginate at about 0.75 of its length. Length 8.5–11.0 mm.

♂.—Mandibular inner margin with tooth (Fig. 25f). Clypeus (Fig. 25f): lobe unusually narrow, distance between lip corners

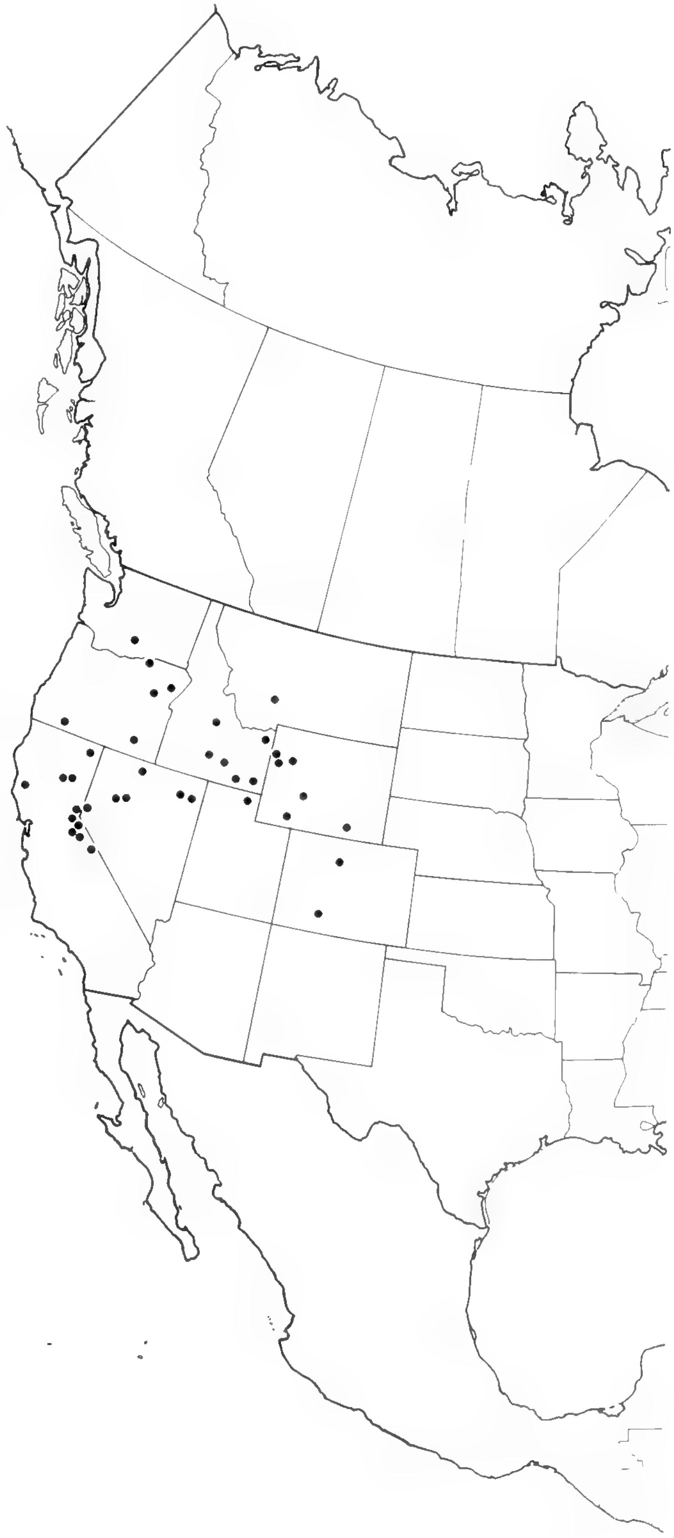

Figure 24 Geographic distribution of *Tachysphex eldoradensis* Rohwer

equal to about 0.6 of clypeal length and to 0.45–0.7 (usually 0.5–0.6) of distance between lip corner and orbit; free margin of lip arcuate; a short carina emerging from each corner; bevel shorter than basomedian area, indistinctly delimited from the latter. Dorsal length of flagellomere I 1.0–1.2 × apical diameter.

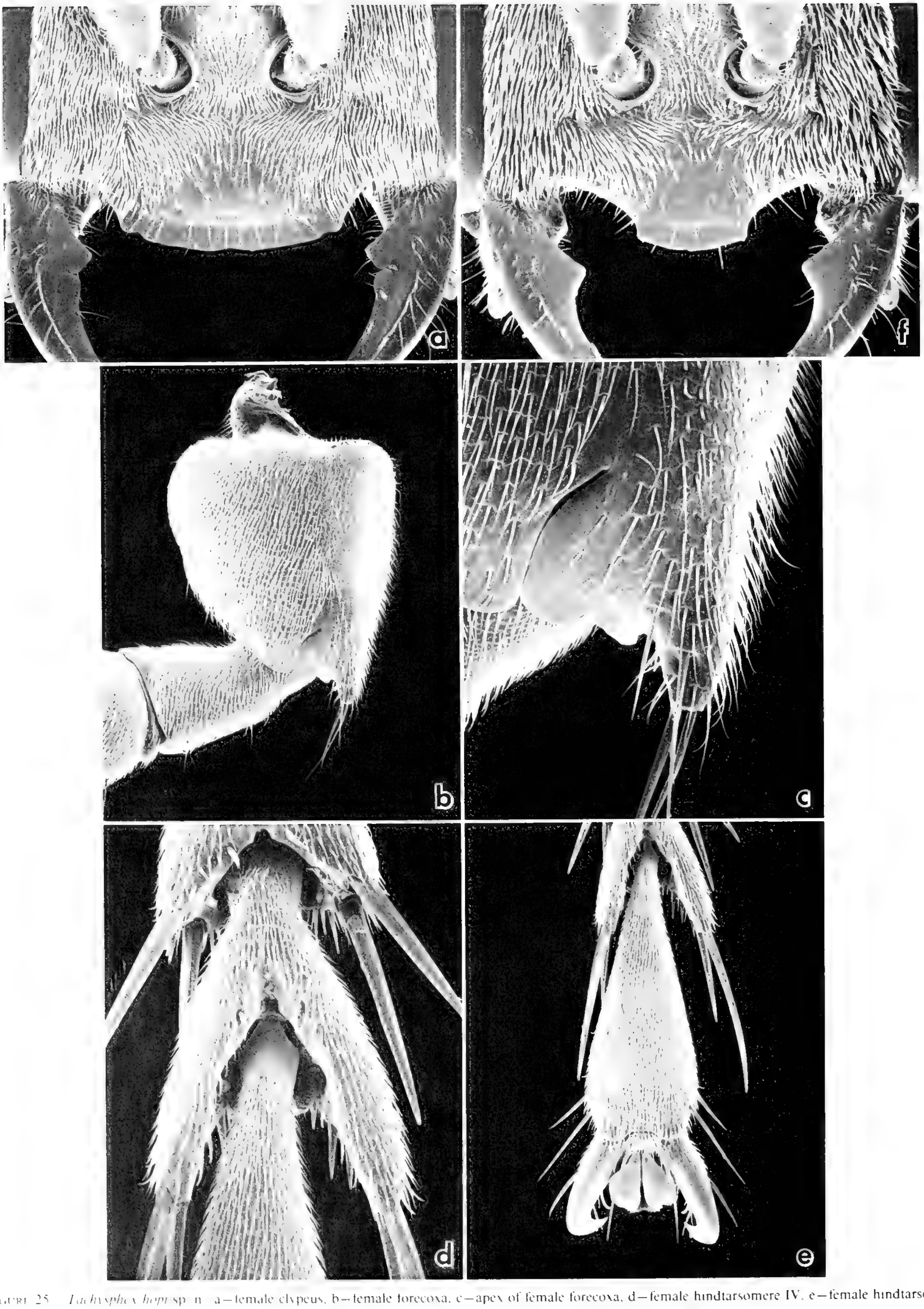

FIGURE 25. *Tachysphex hopi* sp. n.: a—female clypeus, b—female forecoxa, c—apex of female forecoxa, d—female hindtarsomere IV, e—female hindtarsomere V, f—male clypeus.

Vertex width 1.6–1.8× length. Discal punctures of tergum II one to two diameters apart. Sternal punctures about as large as those on the mesothoracic venter; sterna II–IV in most specimens with narrow, impunctate zone apically, but punctate throughout in the single male from Laguna Hanson area, Baja California. Forefemoral notch glabrous. Forebasitarsus with three to five preapical rake spines; outer apical spine of foretarsomere II slightly longer than foretarsomere III. Length 6.5–10.0 mm.

LIFE HISTORY.—Several females from Owinza, Idaho, are pinned with their prey, larvae of *Oedaleonotus aenigma* (Scudder); they are the specimens referred to by Newton (1956). A female from the Bliss area, Idaho, is pinned with an acridid nymph, probably *Aulocara elliotti* (Thomas), det. D. C. F. Rentz. A female from the Saint Anthony area, Idaho, was collected on flowers of *Helianthus annuus* L.

GEOGRAPHIC DISTRIBUTION (Fig. 26).—Western United States north to southern Alberta, south to northern Baja California and Arizona, east to Wyoming and Colorado.

COLLECTING PERIOD.—24 April to 12 June (Mexico), 22 April to 5 August (United States), 25 July to 25 August (Canada).

MATERIAL EXAMINED.—Holotype: ♀, Arizona: Apache Co.: Canyon de Chelly National Monument, White House ruin, 22 June 1975, ASM and WJP (CAS, Type #15911).

Paratypes (127♀, 125♂; specimens for which depository is not indicated below are all in UCD): CANADA: **Alberta:** Medicine Hat, E. H. Strickland (1♀, ANSP); 12 km SW Orion, D. M. McCorquodale (3♀, CAS).

UNITED STATES: ARIZONA: **Coconino:** Flagstaff, R. C. Miller (1♂, CSDA); 10 mi W Jacob Lake, RMB (1♀); Lake Mary, D. R. Estes (1♀, FSCA); Oak Creek Canyon, Englehardt (1♀, MCZ). CALIFORNIA: **El Dorado:** China Flat, F. Bronner (1♀, LACM). **Fresno:** Hume Lake, 5,400 ft, TLG (1♀, TLG); Huntington Lake, NJS (1♀, 1♂, CAS); Los Gatos Canyon, NJS (1♂, CAS). **Humboldt:** North Trinity Mountain, TLG (1♀, TLG). **Inyo:** Big Pine Creek, RMB (1♀). **Kern:** Mt. Pinos, 6,800 ft, JAP (1♀, CIS); Rancheria Creek (Piute Mts.), J. P. and K. E. Donahue (1♀, LACM). **Lassen:** Doyle, EIS (1♂); Hallelujah Junction, RMB (2♀, 2♂; 2♀, CAS), L. D. French (1♀, UCD), J. A. Froebe (3♂), J. S. Glenn (1♂), MEI (1♀, 10♂, UCR; 1♀), D. S. Miller (1♂), R. B. Kimsey and M. L. Siri (1♀, 1♂), C. R. Kovacic (1♀, 2♂), FDP (2♀), JAP (1♀, CIS), JWM (1♀), J. Slansky (1♀, 2♂; 3♂, CAS). **Los Angeles:** 5 mi S Lancaster, EGL and JWMS (1♀, CIS). **Marin:** Point Reyes (Lighthouse), A. M. Barnes (3♀, CIS); Point Reyes, JAP (2♂, CIS). **Mariposa:** Yosemite, EGL (1♀). **Modoc:** 5.5 mi E Cedarville, D. R. Miller (3♂; 1♂, CAS), V. L. Vesterby (3♂). **Monterey:** Marina, coastal sand dunes, MEI (2♂, UCR); Soledad, RMB (1♂); 1 mi S Soledad, R. W. Thorp (1♀, CIS). **Placer:** Carnelian Bay on Lake Tahoe, FDP (1♀). **Plumas:** Chilcoot, J. S. Buckett (1♂), N. B. and W. M. Elliott (1♀, 2♂, NYSU; 1♂, CAS). **Riverside:** Hemet Lake, EIS (1♀). **San Bernardino:** 2 mi E Baldwin Lake, Beesley (1♂, UCR); 2 mi NE Baldwin Lake, S. Freeman (1♀, UCR); Bear Valley, E. C. Van Duzee (1♀); 2 mi W Phelan, J. C. Hall (1♀, 1♂), EIS (1♂); Rock Corral, DKF (1♀, SDNH); Seeley Flat (San Bernardino Mts.), R. May (1♀, LACM). **San Diego:** near Buckman Springs, FXW (1♀, CAS); Warner Springs, RCB (1♀). **San Luis Obispo:** Paso Robles, E. P. Van Duzee (1♂); 10 mi W Simmler, PDH (2♂, CIS). **Sierra:** Yuba Pass, RMB (1♀). **Siskiyou:** Dorris, WJP (1♂, CAS); McBride Springs (3 mi NNE Mt. Shasta town), L. Green (1♂, UCD); Mt. Shasta town, WJP (1♂, CAS). **Tuolumne:** Strawberry, P. D. Ashlock (1♀, USNM), EGL (1♀), JWMS (1♂). **Ventura:** Lockwood Valley, EIS (1♀). COLORADO: **Bent:** 4 mi S Hasty, ASM and WJP (2♀, WJP). **Chaffee:** Salida, R. Roberts (1♀). **Costilla:** Ute Creek (Sage Flats), L. Bruner, named as *neomexicanus* by C. E. Mickel (1♀, UNL). **El Paso:** Colorado Springs, R. and R. Dreisbach (1♀, 9♂; 2♂, CAS). **Huerfano:** Gardner, B. Rotger C. R. (1♀, USNM). **Jackson:** 3 mi E Cowdrey, HEE (1♀, CAS). **Las Animas:** Starkville, collector unknown (1♀). **Weld:** Roggen, HEE (1♀, CAS), collector unknown (1♀, CAS); 1 mi NE Roggen, WJP (5♀, 3♂, CAS). Also the following specimens labeled "Col." (probably Colorado): 1♀, 3♂ (CU), 1♀, 1♂ (USNM). IDAHO: **Blaine:** 3 mi NW Carey, DSH (1♂, UIM). **Camas:** 23 mi E Fairfield, WFB (1♂; 3♂, UIM), DSH (1♀, UIM). **Elmore:** 6 mi S Sunnyside, L. S. Hawkins (1♂, UIM). **Fremont:** Saint Anthony Sand Dunes, MSW (8♀, 3♂, CSDA), R. L. Westcott (1♀, UIM); 6 mi NW Saint Anthony, WFB (1♀, UIM), DSH (1♀), R. L. Westcott (1♂, UIM). **Gooding:** 5 mi N Bliss, JEG (1♀). **Latah:** S slope of Moscow Mt., DSH (1♀, UIM). **Lemhi:** Lemhi Pass, WFB (1♂, UIM). **Lincoln:** Owinza, Lee Seaton (7♀, USNM); Shoshone, R. L. Newton (3♀, 6♂, USNM); 18 mi E Shoshone, R. C. Newman (1♀, 2♂, USNM). **Madison:** Lincoln, R. C. Newton (2♂, USNM). **Owyhee:** Little Valley (18 mi SW Bruneau), A. R. Gittins (1♂, UIM). MONTANA: **Gallatin:** Three Forks, E. C. Van Duzee (8♀; 1♂, CAS). NEVADA: **Eureka:** Diamond Valley, P. C. Martinelli (1♀, NSDA). **Humboldt:** Orovada, FDP (1♂). **Washoe:** 1 mi S Mustang, FDP (1♀, NSDA), Red Rock, RCB (2♀, USU), Reno, FDP (2♂, NSDA), 15 mi E Reno, RMB (1♀), MEI (1♀); Verdi, RMB (2♂, 1♂ CAS), E. J. Montgomery (1♂). OREGON: **Harney:** Virginia Valley, 30 mi SW Follyfarm (S end of Alvord Desert), H. A. Scullen (1♂). **Jackson:** Ashland Mt. (above timberline), H. A. Scullen

FIGURE 26. Geographic distribution of *Tachysphex hopi* sp. n.

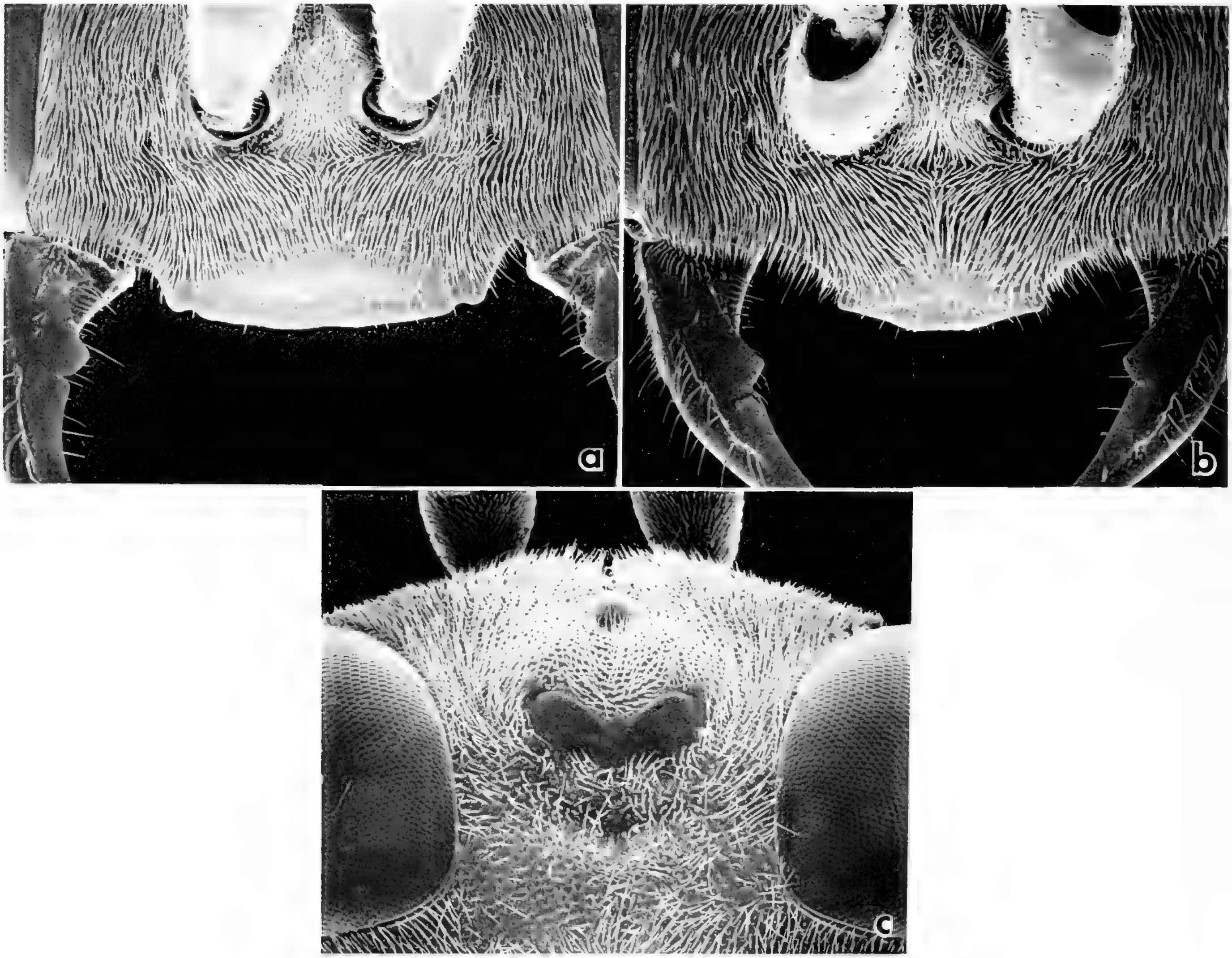

FIGURE 27. *Tachysphex pechumani* Krombein: a—female clypeus; b—male clypeus; c—male vertex.

(1♂). **Klamath:** Crater Lake National Park, J. Schuh (1♂). **Lincoln:** Owynza, JEG (1♂). **Morrow:** Boardman, G. R. Ferguson (2♂, 4♂, 1♂, CAS). **Umatilla:** "Camp Umatilla, W. T., June 26, '82," collector unknown (1♂, MCZ), Hermiston, collector unknown (1♂). UTAH: **Cache:** Cornish, GEB (13♂; 2♂, CAS, 3♂, USU), RMB (1♀), FDP and D. Vincent (1♂, USU). **Grand:** 25 mi S Moab, GEB and R. Brumley (1♀, WJP, 1♂). **Washington:** Zion National Park, collector illegible (1♂, USU). Also Salt Lake (county not indicated), collector unknown (1♂). WASHINGTON: **Benton:** 2 mi S Pasco, E. D. Dailey (1♂, WSU). **Garfield:** Snake River 4 mi below Lower Granite Dam, J. Jenkins (1♂, CAS). **Okanogan:** Okanogan, DSH (1♂, UIM). **Yakima:** N Yakima, E. Jenne (2♂, WSU). WYOMING: **Sweetwater:** Green River, collector unknown (1♂, AMNH). **Teton:** Gridger Basin, S. Garman (1♀, MCZ).

MEXICO: **Baja California Norte:** 12.3 mi S El Cóndor, DKF (1♀, SDNH); Sierra Juarez 6 mi N Laguna Hanson, collector unknown (♂, SDNH).

Tachysphex pechumani Krombein

(Figures 27, 28)

Tachysphex tarsatus subsp. *pechumani* Krombein, 1938:468, ♀, ♂. Holotype ♀, New Jersey, Ocean Co., Manahawkin (USNM).—As *Tachysphex pechumani*: G. Bohart 1951:952 (new status). Krombein 1967:393. Kurczewski et al. 1970:1594 (♂). Bohart and Menke 1976:275. Kurczewski and Elliott 1978:765–780. Krombein 1979:1629.

DIAGNOSIS.—*Tachysphex pechumani* occurs in Michigan and New Jersey. The female has a brassy golden frontal vestiture, a character that distinguishes it from other species of the *pompiliformis* group except *bohartorum*, *psilocerus*, and *scopaeus* (some other species may have a golden tinge). The unspecialized upper metapleuron of *pechumani* separates it from *psilocerus* and *scopaeus*, and the following characters differentiate it from *bohartorum*: the shallowly incised clypeal lip (Fig. 27a), the flagellum largely red or at least reddish brown, the posterior (horizontal) part of the mesothoracic venter longer than the anterior (oblique) part, the forecoxa not expanded into a process apically, tarsomeres IV and V are not elongate, and gastral apex black. The broad vertex (width twice length) is an additional diagnostic feature.

In males of *pechumani* the unusually broad vertex (width: length ratio 2.1–2.3) is distinctive (Fig. 27c), but the vertex width is also more than twice length in other species (at least in occasional specimens). These differ from *pechumani* in having the characters listed in parentheses: *antennatus* (vertex setae appressed), *crassiformis* (expanded axilla), *glabrior* (punctate mesopleuron), *idiotrichus* (unusually long vestiture, compressed forefemoral notch), *psammobius* (punctate mesopleuron, triangular clypeal lip), *punctifrons* (peculiar mesopleural carinae), and *scopaeus* (punctate mesopleuron, peculiar metapleuron).

DESCRIPTION.—Frons, vertex, and scutum punctate, punc-

tures nearly contiguous. Mesopleuron opaque, microsculptured, shallowly, indistinctly punctate. Propodeal dorsum evenly microareolate, side microsculptured, not ridged; hindface at most with a few, inconspicuous ridges. Discal micropunctures of tergum II about one diameter apart. Sternum I apically at most with shallow, indistinct depression. Hindcoxa not carinate.

Vestiture partly obscuring integument between antennal socket and orbit. Vertex setae erect (suberect posteriorly in female), 1.0 MOD long. Terga I–IV or I–V silvery fasciate apically. Scutal and femoral setae appressed.

♀.—Clypeus (Fig. 27a): bevel shorter than basomedian area; lip broadly arcuate, shallowly incised laterally. Dorsal length of flagellomere I 2.0–2.4 × apical width. Vertex width twice length. Tergum V densely punctate, its apical depression impunctate in some individuals. Pygidial plate alutaceous, punctate. Trochanteral and femoral punctures fine, subcontiguous. Length 9–11 mm.

Head and thorax black; flagellomeres II–X or III–X reddish brown to orange red (yellow in live specimens according to F. E. Kurczewski, pers. comm.), III–V infumate beneath in some specimens. Gastral segment I and II or I–III red, remainder black. Legs black, tarsal apex reddish. Clypeal and frontal vestiture brassy golden. Wings moderately infumate.

♂.—Mandibular inner margin with tooth (Fig. 27b). Clypeus (Fig. 27b): bevel shorter than basomedian area; lip arcuate or slightly sinuate; its corners rectangular to obtuse, separated by a distance that equals 0.9–1.1 of distance between corner and orbit. Dorsal length of flagellomere I 1.1–1.4 × apical width. Vertex width 2.1–2.3 × length (Fig. 27c). Sterna densely punctate throughout. Forefemoral notch glabrous. Forebasitarsus with two or three preapical rake spines. Outer apical spine of foretarsomere II as long as tarsomere III. Length 6–10 mm.

Body black, including legs, but terga I–III in some specimens with small, reddish zones. Frontal vestiture silvery. Wings faintly infumate.

Life History.—*Tachysphex pechumani* has been studied in detail by Kurczewski and Elliott (1978). There is one generation per year. Females nest in sandy or gravelly soil (Krombein 1967). Females searching for a nesting site: (1) walk relatively slowly, (2) pause abruptly and make zigzag turns (so that movements appear jerky), (3) keep antennae bowed, tapping the tips alternately on the soil, occasionally raising and waving them, and (4) keep wings flat over the gaster, raising them to an angle of about 45° with the dorsum before taking flight. When starting a nest, the female first breaks the sand crust with her mandibles, then she digs a burrow with her forelegs which work in unison. She periodically removes the sand that has accumulated by raking it backwards with her forelegs. The sand finally forms a flattened, fan-shaped tumulus. The burrow, 6 mm in diameter and 45–85 mm long, enters the soil at an angle of 10–30° to the surface. It ends in a single cell, which is 20–40 mm beneath the surface. After completion, the nest is temporarily closed, although the closure may be incomplete (the entrance frequently remains open at the top). After closing the nest, the female periodically walks back to the nest, examines the entrance, turns, and walks away. Probably these are efforts to memorize the nest location. The observed prey are nymphal and adult acridids: *Orphulella pelidna* (Burmeister), *Melanoplus impudicus* Scudder, *fasciatus* (Walker), and *sanguinipes* (F.). The acridids are paralyzed by one to three stings (this observation may be inaccurate). Paralysis is incomplete: the prey dug out of the wasp's nest move their mouthparts, antennae, and occasionally other appendages, and breathing movements of their abdominal segments are visible. Heavy prey (more than twice the female weight) are transported on the ground but lighter prey are flown to the nest. During ground transport, the female walks on her fore- and midlegs, and proceeds forward. The prey is straddled venter up; its antennae are held with her mandibles, and its body is clutched by her hindlegs. It is dropped at the nest entrance, venter up and head toward the nest. The female then opens the nest, enters, reappears headfirst, grasps the prey's antennae with her mandibles, and drags it inside. Only one prey per cell was found in fully provisioned cells. Prey position in the cell is venter up and head inward. The wasp's egg is attached by its caudal end "to the forecoxal corium of the prey."

Geographic Distribution (Fig. 28).—*Tachysphex pechumani* is known from two isolated areas: the Pine Barrens in southern New Jersey and the Lower Peninsula of Michigan. Both areas (except Saginaw Co., Michigan) are mainly dry, sandy soils covered with pine forest. G. Bohart (1951) lists New York State for this species, but neither I nor F. E. Kurczewski (pers. comm.) have seen material from that area, and Kurczewski and Elliott (1978) were unable to find *pechumani* in pine-barren areas of upstate New York and Long Island.

Material Examined.—47♀, 84♂ (AMNH, CAS, CSU, CU, KVK, MCZ, MOB, UCD, UMMZ, USNM)

Records.—UNITED STATES: MICHIGAN: **Allegan:** Allegan State Game Area **Cheboygan:** Douglas Lake. **Crawford, Gladwin, Gratiot, Iosco, Kalkaska, Midland, Montcalm, Saginaw:** —. **Oakland:** Farmington. **Washtenaw:** Pinckney State Recreation Area near Half Moon Lake. NEW JERSEY: **Atlantic:** Weymouth, Elwood (Kurczewski et al. 1970; Kurczewski and Elliott 1978). **Burlington:** Browns Mills, Chatsworth, Lebanon State Forest, New Gretna, Ong, Rancocas Park, Vincentown (Kurczewski et al. 1970). **Camden:** Atco, Clementon. **Cape May:** 3 mi S Seaville **Cumberland:** Manumuskin, Vineland (Maurice River). **Gloucester:** Iona (Kurczewski et al. 1970). **Ocean:** Lakehurst (Wrangle Brook Road), Manahawkin

Tachysphex bohartorum Pulawski

(Figures 28–30)

Tachysphex bohartorum Pulawski, 1982:30, ♀, ♂. ! Holotype: ♀, California: Nevada Co.: Boca (UCD)

Diagnosis.—The female of *bohartorum* differs from most New World species in having a distinctive mesothoracic venter: the posterior, horizontal part is shorter than the anterior, oblique part (the mesothorax of *hopi* and *occidentalis* approaches this condition). Like the female of *hopi* and many *occidentalis*, the forecoxa is expanded into an apicomedian process (Fig. 29b, c), and tarsomeres IV and V (Fig. 29d, e) are unusually long (unlike *occidentalis*, the hindfemur of *bohartorum* is all black, and the clypeal lip is incised laterally). Like *pechumani*, it has brassy golden frontal vestiture, but unlike that species the gaster of *bohartorum* is all red and the flagellum is all black. The frontal vestiture is also golden in *psilocerus* and *scopaeus*, but these species have a distinctive upper metapleuron (flange broad, an oblique lamella extending from its fore end). The male of *bohartorum* can be recognized by the closely punctate terga (punctures almost contiguous) combined with the apicomesally impunctate and glabrous sterna II–IV (Fig. 30a–c).

Supplementary diagnostic characters of *bohartorum* are: propodeum not ridged (at most the hindface has a few, inconspicuous ridges below); setae of propodeal dorsum appressed mesally, oriented obliquely anterad; female tergum V entirely punctate.

Description.—Punctures subcontiguous on frons, vertex,

FIGURE 28. Geographic distribution of *Tachysphex pechumani* Krombein and *bohartorum* Pulawski.

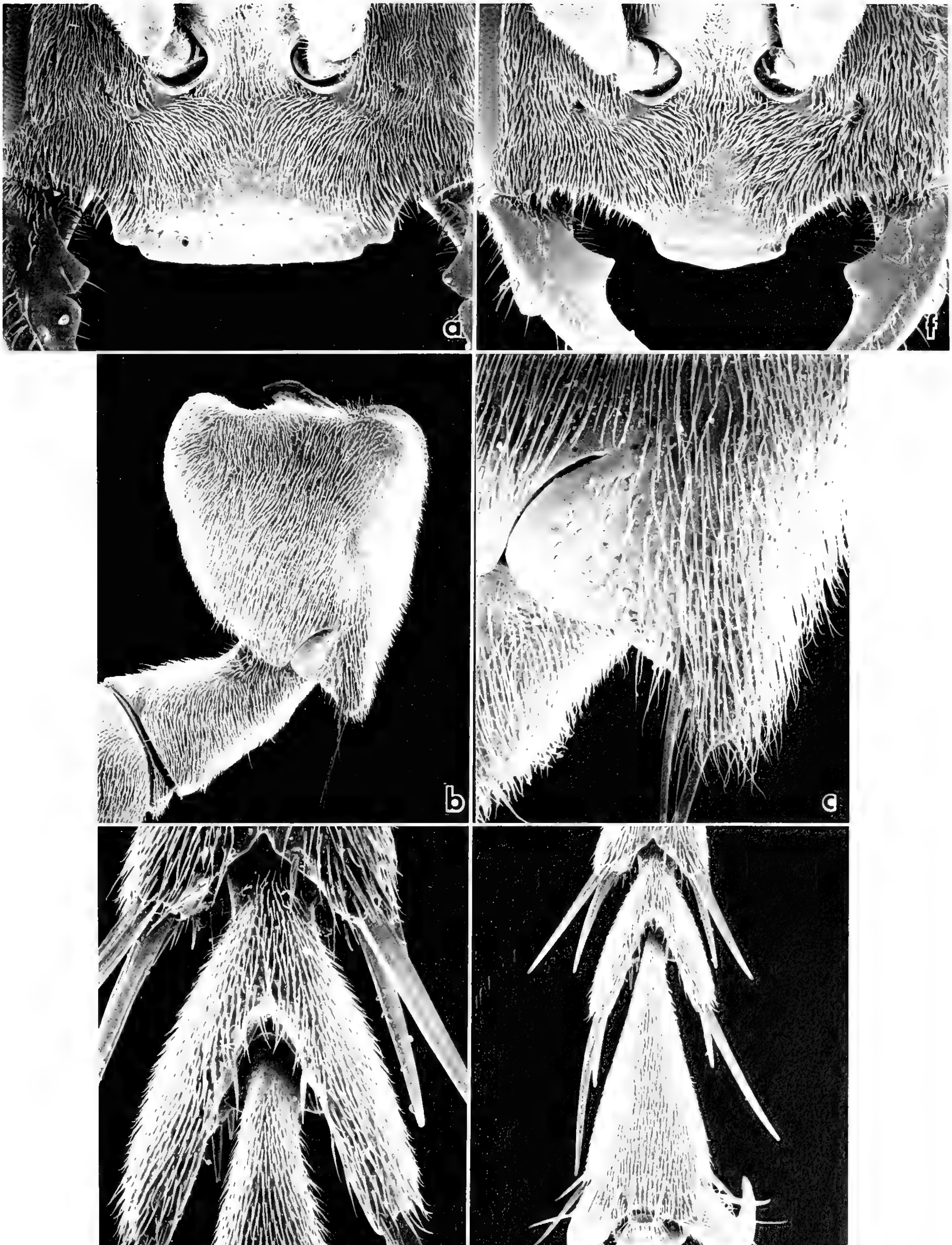

FIGURE 29. *Tachysphex bohartorum* Pulawski, female. a—female clypeus, b—forecoxa, c—apex of forecoxa, d—hindtarsomere IV, e—hindtarsal apex, f—male clypeus

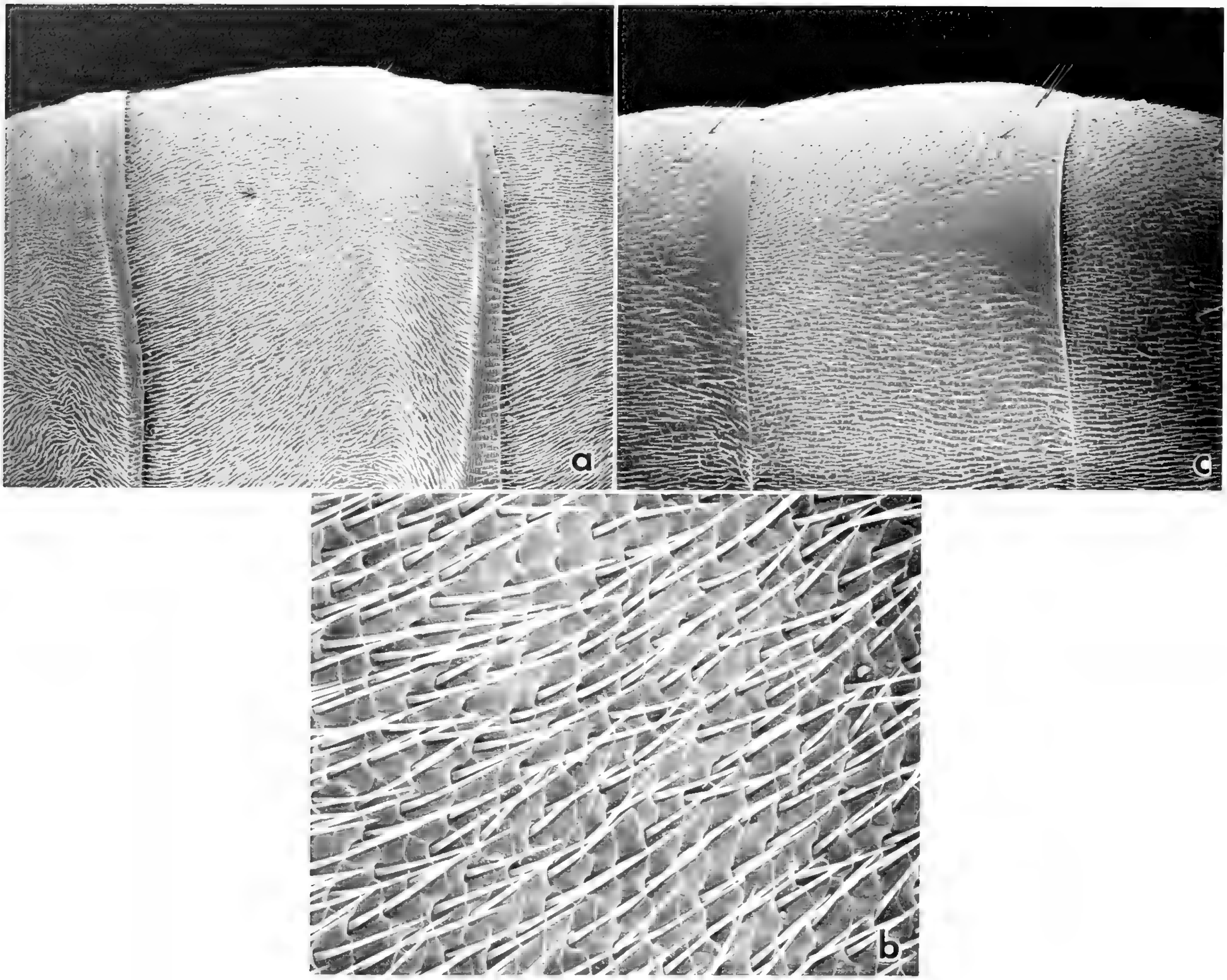

FIGURE 30. *Tachysphex bohartorum* Pulawski, male: a—tergum II; b—sculpture of tergum II; c—sternum III.

mesothorax, trochanters, and femora. Mesopleuron dull, microsculptured, its punctures shallow, ill defined. Propodeum microareolate, at most hindface with a few, inconspicuous ridges beneath; dorsum usually with median carina of varying length. Sternum I apically at most with shallow, indistinct depression. Terga I–V (female) or I–VII (male) evenly, closely punctate throughout, punctures mostly subcontiguous. Hindcoxa not carinate.

Integument obscured by vestiture (not totally so in smallest specimens) between antennal socket and orbit. Setae: appressed on mesothorax and femora except subappressed on hypoepimeral area; on vertex subappressed to (some male) erect, shorter than MOD; on scutum at middle oriented posterad or posterolaterad; on propodeal dorsum mesally appressed, oriented anterolaterad.

Head, thorax, and legs black, tarsi (except basally) reddish. Gaster red or (some males) segments IV–VII dark brown. Terga I–IV silvery fasciate apically (tergum IV only weakly so). Wings infumate.

♀.—Clypeus (Fig. 29a): bevel about as long as basomedian area; lip free, margin straight or slightly concave, deeply incised laterally. Dorsal length of flagellomere I 2.3–2.6 × apical width. Vertex width about 1.8 × length. Mesothoracic venter peculiar: its posterior, horizontal part shorter than anterior, oblique part. Pygidial plate alutaceous, punctate. Forecoxa with apicomedian process (Fig. 29b, c). Tarsomeres IV and V unusually long (Fig. 29d, e). Length 9–11 mm.

Clypeal and frontal vestiture brassy golden.

♂.—Mandibular inner margin with tooth (Fig. 29f). Clypeus (Fig. 29f): bevel equal to basomedian area or shorter; lip arcuate or (some specimens) sinuate, its corners rectangular to obtuse; distance between corners equal to 0.7–0.8 of clypeal length and of distance between corner and orbit; longitudinal carina emerging from each corner and extending dorsad slightly beyond lip base. Dorsal length of flagellomere I 1.3–1.5 × apical width. Vertex width 1.7–1.9 × length. Tergal punctures unusually dense (Fig. 30a, b); sternal punctures about as large as those on mesothoracic venter; sternum III impunctate posteromesally, sterna

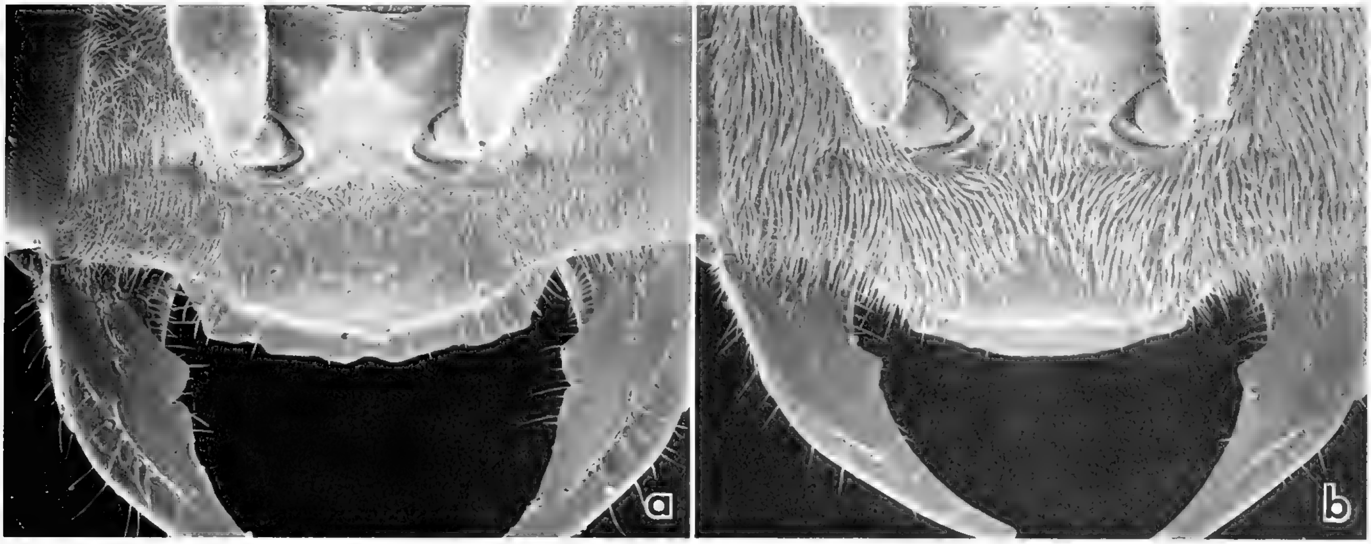

FIGURE 31. *Tachysphex irregularis* Pulawski: a—female clypeus; b—male clypeus.

II–IV impunctate on apical depression (Fig. 30c), at least mesally. Forefemoral notch glabrous. Forebasitarsus with two or three preapical rake spines; outer apical spine of foretarsomere II longer than foretarsomere III. Length 5–8 mm.

Frontal vestiture silvery or with golden tinge.

GEOGRAPHIC DISTRIBUTION (Fig. 28).—North and central Sierra Nevada (both in California and Nevada) and adjacent mountain ranges in northern California and southern Oregon.

MATERIAL EXAMINED.—98♀, 285♂.

RECORDS.—UNITED STATES: CALIFORNIA: **Alpine:** Carson Pass, Hope Valley, 15 mi NE Red Lake, Winnemucca Lake, Woodfords. **Del Norte:** Little Grayback (NE part of county). **El Dorado:** Echo Pass, Echo Lake, Echo Portal, Fallen Leaf Lake, Kyburz Flat, Meyers, Tahoe, Strawberry Valley. **Humboldt:** Red Cape Lake. **Inyo:** Big Pine Creek, near Mono Pass (12,000 ft). **Lassen:** Bridge Creek Camp, Summit Camp (E Lassen Peak). **Mariposa:** Sentinel Dome Cutoff (Yosemite National Park). **Modoc:** 2 mi W Cave Lake, Cedar Pass (Warner Mts.), Warner Mts. 2 mi NNW Fort Bidwell. **Mono:** 11 mi N Bridgeport, East Walker River (13 mi NE Bridgeport), Leavitt Meadow, Parker Creek (8 mi S Lee Vining), S Fork Cottonwood Creek (Sweetwater Mts.). **Nevada:** Boca, Sagehen Creek near Hobart Mills. **Placer:** Carnelian Bay (Lake Tahoe), Devil's Peak, Tahoe (also 2 mi NE). **Plumas:** Bucks Lake, Lake Almanor, Meadow Valley, 14 mi W Quincy. **Shasta:** Lake Eiler (ca. 20 mi S Burney), Lassen Peak, Tamarack Lake. **Sierra:** Independence Lake, Sierra Buttes, Sierra Valley, Sierraville, Yuba Pass. **Siskiyou:** 1 mi E Ash Creek Ranger Station (9 mi E McCloud), Martin's Dairy (8 mi NW Macdoel), McBridge Springs (3 mi NNE Mt. Shasta town), Mt. Shasta town, 1 mi SE Salmon Mt. **Trinity:** Coffee Creek Ranger Station. **Tuolumne:** Chipmunk Flat (3 air mi W Sonora Pass), Dardanelle, Sonora Pass. NEVADA: **Douglas:** Spooners Lake N Junction Hwy. 28. **Washoe:** Mt. Rose. OREGON: **Jackson:** 8 mi SE Butte Falls, Mt. Ashland. **Klamath:** 15 mi NE Bly, Eagle Ridge near Klamath Lake, Lake of the Woods. **Lake:** Warner Pass

Tachysphex irregularis Pulawski

(Figures 31, 32)

Tachysphex irregularis Pulawski, 1982:31, ♀, ♂. ! Holotype: ♀, California: Lassen Co.: Hallelujah Junction (UCD).

DIAGNOSIS.—*Tachysphex irregularis* differs from other members of the *pompiliformis* group in having a rugose or punctatorugose mesopleuron. Additional recognition features are: trochanteral venter almost impunctate in most females, and in the male: graduli present on sterna III–VI, sternal punctures about as large as those on the mesothoracic venter.

DESCRIPTION.—Punctures shallow, subcontiguous on frons and vertex; less than one diameter apart on scutum (but many discal punctures more than one diameter apart in some specimens). Mesopleuron punctatorugose or rugose. Propodeal dorsum evenly microareolate, side ridged in most specimens, hindface ridged. Sternum I without apical depression. Hindcoxa carinate basally.

Setae appressed on scutum and midfemoral venter, on scutum at middle oriented almost uniformly posterad.

Head and thorax black. Terga I–V silvery fasciate apically (fascia of female tergum V broadly interrupted). Wings weakly infumate.

♀.—Clypeus (Fig. 31a): bevel longer than basomedian area; lip varying, mainly with median emargination and with one lateral indentation on each side, but simply arcuate in some specimens. Dorsal length of flagellomere I 2.4–2.7× apical width. Punctures of mesothoracic venter about one diameter to (some specimens) many diameters apart. Most micropunctures of tergum II at middle about one diameter apart. Tergum V densely punctate (except mesally), but apical depression impunctate. Pygidial plate shiny, sparsely punctate. Trochanteral venter shiny, with scattered punctures (but punctures close to each other in a female from Las Cruces, New Mexico, UCD). Forefemoral punctures fine, dense (two to three diameters apart in most specimens). Length 8–11 mm.

Integument not hidden under vestiture between antennal socket and orbit. Vertex setae about 0.5 MOD long, subappressed posteriorly, suberect anteriorly.

Gaster red. Legs usually black, with reddish tarsal apex, but in occasional specimens the following are red: hindfemur, hindtibia, and partly fore- and midtibia. Frontal vestiture silvery or with golden tinge.

♂.—Mandibular inner margin with tooth (Fig. 31b). Clypeus (Fig. 31b): bevel shorter to longer mesally than basomedian area; lip arcuate, its corners usually closer to orbits than to each other, but slightly closer to each other than to orbits in some individuals. Dorsal length of flagellomere I 1.7–2.0× apical width. Vertex width 1.5–1.9× length. Sternal punctures conspicuous,

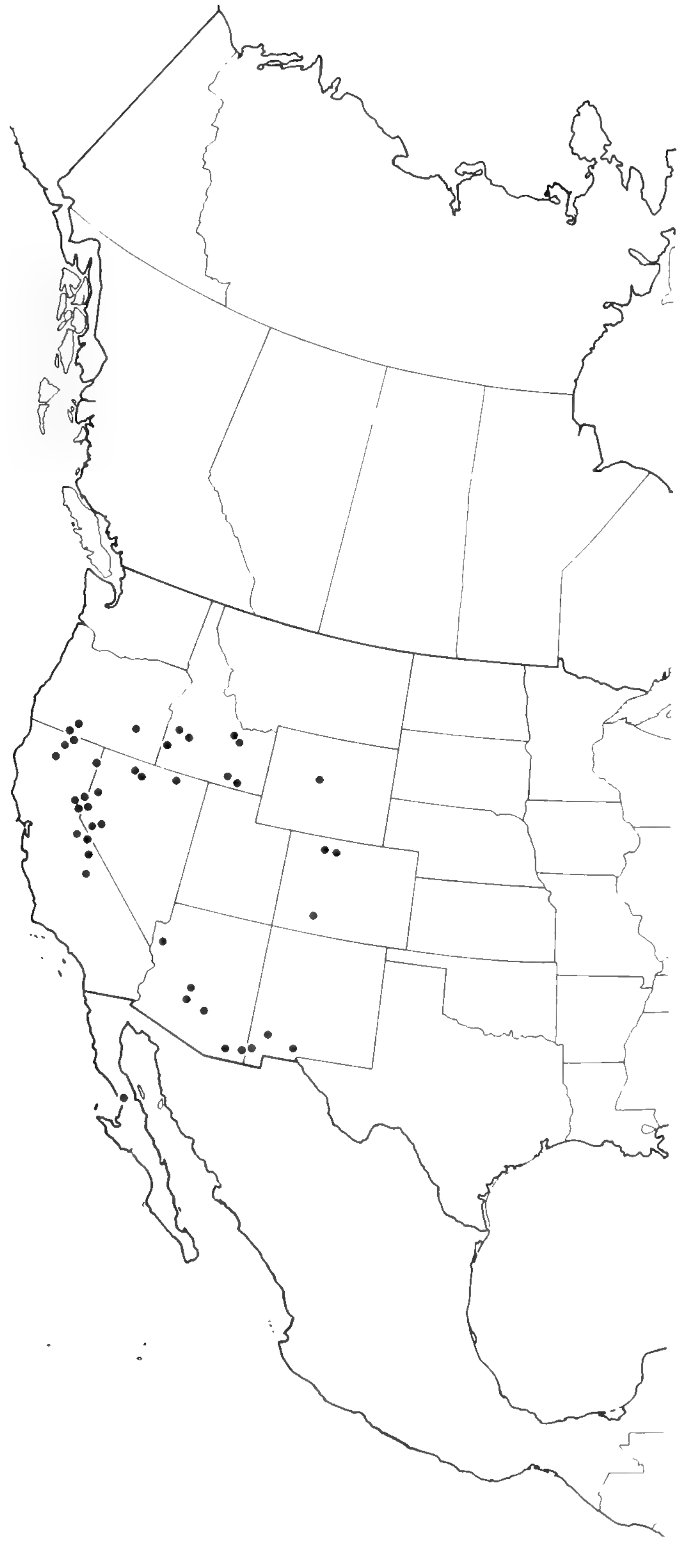

FIGURE 32. Geographic distribution of *Tachysphex irregularis* Pulawski.

about as large as those on mesothoracic venter, subcontiguous or up to two or three diameters apart mesally; sterna III–VI with graduli. Forefemoral notch finely pubescent. Forebasitarsus with none to four preapical rake spines that are at most scarcely longer than basitarsal width; outer apical spine of forebasitarsus II much longer than forebasitarsus III. Length 7.5–10.5 mm.

Integument totally hidden under vestiture between antennal socket and orbit when seen from certain angles. Vertex setae erect, 0.5–0.7 MOD long.

Gastral segments I–III red, remainder black (only segments I and II or II and III red in some individuals). Legs black, tarsal apex brown. Frontal vestiture silvery.

GEOGRAPHIC DISTRIBUTION. (Fig. 32).—Western United States, eastward to Wyoming and New Mexico, also Baja California Norte.

MATERIAL EXAMINED.—65♀, 45♂ (AMNH, CAS, CIS, CSDA, CSU, FSCA, MCZ, TLG, UAT, UCD, UIM, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** 8 mi NE Apache, 14 mi W Tombstone. **Maricopa:** Rainbow Valley, route 74 (5 mi W route 17). **Mohave:** 4 mi W Chloride, Kingman. **Pinal:** 8 mi SE Olberg. CALIFORNIA: **Inyo:** Bishop, Whitney Portal. **Lassen:** Hallelujah Junction. **Modoc:** 5.5 mi E Cedarville, Hot Creek. **Mono:** Benton Crossing. **Nevada:** Boca, Sagehen Creek near Hobart Mills. **Sierra:** Sattley. **Siskiyou:** Dorris, Macdoel, Hatfield, Mt. Shasta town, Red Rock. **Tuolumne:** Sonora Pass. COLORADO. **Jackson:** 10 mi N junction of roads 14 and 40. **Mineral:** South Clear Creek. **Routt:** 7 mi E Hayden. IDAHO: **Butte:** 6 mi S Howe (also 7 mi E). **Canyon:** Nampa. **Cassia:** 4 mi SE Malta (also 5 mi N). **Custer:** 2 mi E Leslie. **Elmore:** 4 mi E Orchard. **Oneida:** 5 mi NW Holbrook. **Owyhee:** Silver City (also 17 mi W). NEVADA: **Elko:** Cobb Creek (6 mi SW Mountain City). **Humboldt:** Orovada, Paradise City (also 15 mi E). **Lyon:** Smith. **Mineral:** 4.5 mi S Schurz. **Washoe:** Pyramid Lake, Reno Hot Springs, Sky Ranch near Reno. NEW MEXICO: **Dona Ana:** Las Cruces. **Grant:** Hurley. **Hidalgo:** Rodeo. OREGON: **Harney:** "P" Ranch. **Klamath:** 3 mi S Chiloquin, Lower Klamath Lake. WYOMING: **Fremont:** Shoshoni.

MEXICO: **Baja California Norte:** 4 mi NE El Rosarito (28°42′N, 113°58′W), 6 mi NE Santa Rosalillita (28°45′N, 114°10′W).

Tachysphex laevifrons (F. Smith)

(Figures 33, 36)

Larrada laevifrons F. Smith, 1856:291, ♀. ! Holotype: ♀, Florida: Duval Co.: St. John's Bluff, now Jacksonville (BMNH, London).—In *Larra:* Cresson 1862: 237, Patton 1881:389, Kohl 1885:245, Provancher 1887:267 (♂); W. Fox 1894*a*: 492, Dalla Torre 1897:669 (as *levifrons*).—As ?*Tachysphex:* Ashmead 1899: 250, Harrington 1902:221.—In *Tachysphex:* G. Bohart 1951:951; Krombein 1958*c*:188, Kurczewski 1966*b*:439, 445, Krombein 1967:393; Kurczewski 1971: 114, Bohart and Menke 1976:274, Krombein 1979:1628.

Tachysphex leensis Rohwer, 1911:578, ♂. ! Holotype: ♂, Texas: Lee Co.: no specific locality (USNM). Synonymized by Pulawski *in* Krombein 1979:1628.—G. Bohart 1951:951, Bohart and Menke 1976:274.

Tachysphex consimiloides Williams, 1914:164, ♀. ! Holotype: ♀, Kansas: Barton Co.: no specific locality (KU). Synonymized by G. Bohart 1951:951 (with *Tachysphex leensis*).—LaBerge 1956:527, Arnaud 1970:32.

DIAGNOSIS.—*Tachysphex laevifrons* can be recognized by the combination of appressed mesothoracic vestiture and a uniformly microareolate mesopleuron and propodeum, including hindface (mesothoracic vestiture is also appressed in *musciventris, tarsatus, williamsi,* and many *antennatus,* but their thorax is differently sculptured). Sternum II of the female is uniformly micropunctate, including the apical depression (the only such case in North American *Tachysphex*). The absence of a glabrous clypeal bevel in some females is also diagnostic (Fig. 33a). The male differs from *musciventris* and *antennatus* in having an arcuate, moderately broad clypeal lip (lobe triangular in *musciventris,* unusually broad in *antennatus*), and from *tarsatus* and *williamsi* in having appressed sternal setae.

DESCRIPTION.—Frons opaque, finely punctate (punctures subcontiguous) to irregularly microrugose. Vertex finely, evenly punctate, punctures less than one diameter apart, often subcon-

FIGURE 33. *Tachysphex laevifrons* (F. Smith): a—female clypeus; b—male clypeus.

tiguous. Mesopleuron and all propodeum opaque, evenly microareolate. Discal micropunctures of tergum II less than one diameter apart. Hindcoxa not carinate.

Vestiture short, decumbent on frons, mesothorax, and femora. Vertex setae appressed, but erect (about 1.0 MOD long) on postocellar impression in some populations. Middle scutal setae oriented posterad.

Head, thorax, and legs black, tarsal apex brownish. Terga I–III red (sometimes I and II only), usually also corresponding sterna; remainder black; terga I–IV silvery fasciate apically. Wings weakly infumate. Frontal vestiture silvery.

♀.—Clypeus (Fig. 33a): bevel absent to about as long as basomedian area; lip arcuate, without mesal notch or lateral incisions. Dorsal length of flagellomere I 1.8–2.0× apical width. Vertex slightly narrower to slightly wider than long. Sternum II densely punctate throughout, sometimes also sternum III; tergum V densely punctate, including apical depression. Forefemoral and trochanteral venter finely, evenly punctate, punctures less than one diameter apart. Length 7–10 mm.

Vestiture partly obscuring integument between antennal socket and orbit.

♂.—Inner mandibular margin with tooth (Fig. 33b). Clypeus (Fig. 33b): bevel absent; lip broadly arcuate, its corners obtuse, much closer to orbit than to each other. Dorsal length of flagellomere I 1.1–1.2× apical width. Vertex width 1.6–1.7× length. Sterna densely punctate throughout. Forefemoral notch almost glabrous. Foretarsus with rake; outer apical spine of foretarsomere II equal to tarsomere III or longer. Length 6.0–7.5 mm.

Frontal vestiture weak to dense, integument visible or obscured between antennal socket and orbit.

VARIATION.—Specimens from the Carolinas and Florida have an opaque, uniformly microsculptured scutum; the setae on the postocellar impression are erect, about 1.0 MOD long. Individuals from Kansas, Oklahoma, and Texas usually have the scutum finely, very closely punctate, and the setae on the postocellar impression are appressed. The latter population could be called *laevifrons leensis* by those who accept trinominal nomenclature.

LIFE HISTORY.—Females of *laevifrons* nest in flat or slightly sloping sand and prey on immature *Melanoplus* (Acrididae) according to Krombein (1967). There is one generation per year (Kurczewski 1971), and the nest is unicellular (Kurczewski 1966*b*). Kurczewski (1966*b*) also noted that the species is not gregarious and that territoriality was not apparent between males.

GEOGRAPHIC DISTRIBUTION (Fig. 36).—United States east of 100th meridian, north to North Carolina and Kansas; it replaces *tarsatus* in the southeast.

MATERIAL EXAMINED.—74♀, 29♂ (BMNH, CAS, CU, FSCA, GEB, INHS, KU, MCZ, NYSU, TAI, UCD, UCR, UGA, USNM).

RECORDS.—UNITED STATES: FLORIDA: **Alachua:** Alachua, Gainesville, 6 mi S La Crosse, Monteoca (11 mi NW Gainesville). **Clay:** Camp Crystal. **De Soto:** Arcadia. **Duval:** Jacksonville, including St. John's Bluff. **Highland:** Lake Placid. **Lake:** —. **Orange:** Orlando. **Putnam:** Welaka. **Suwannee:** Suwannee River State Park. **Taylor:** Perry. KANSAS: **Barton:** —. **Stafford:** Salt flats area. NORTH CAROLINA: **Cumberland:** Fort Bragg. **Dare:** Nag's Head. **Moore:** Southern Pines. OKLAHOMA: **Beaver:** Forgan. SOUTH CAROLINA: **Georgetown:** 6 mi SSW Murrell's Inlet. TEXAS: **Kenedy:** 3 mi S Sarita. **Kleberg:** 6 mi E Riviera. **Lee:** Fedor. **Victoria:** Victoria

Tachysphex tarsatus (Say)

(Figures 34–36)

Larra tarsata Say, 1823:78, sex not indicated. Holotype or syntypes: Arkansas: no specific locality (destroyed, see W. Fox 1902:11).—F. Smith 1856:281; Cresson 1862:237; Riley 1880:270; Patton 1881:389; Ashmead 1890:33.—In *Larrada:* Cresson 1865:464, 1876:208.—In *Tachysphex:* W. Fox 1894*a*:512, 1894*b*: 106; Dalla Torre 1897:685; Ashmead 1899:250; J. Smith 1900:518; Peckham and Peckham 1900:89, 1905:261; H. Smith 1908:381; J. Smith 1910:683; Rohwer 1911:580 (in key); Williams 1914:165, 203; Rohwer 1916:687; Stevens 1917:422; Mickel 1918:422; Bradley 1928:1009; Robertson 1928:128, 195; Brimley 1938:443; Strickland 1947:129; Krombein 1950:267; G. Bohart 1951: 952; Cooper 1953:33; Krombein 1953*a*:330; Kurczewski and Kurczewski 1963: 146; Kurczewski 1966*b*:436–453; Krombein 1967:393; Evans 1970:490; Alcock and Gamboa 1975:164; Bohart and Menke 1976:277; Krombein 1979:1630; Steiner 1981:333, 1982:2, 12–14; Finnamore 1982:106; Elliott and Kurczewski 1985:293; Rust et al. 1985:46

DIAGNOSIS.—Females of *tarsatus* and *williamsi* cannot be distinguished from one another. Both have appressed mesopleural setae, including hypoepimeral setae (Fig. 34b). Appressed setae also occur in *laevifrons*, *musciventris*, some *antennatus*, and some *crassiformis*, which have distinctive characters easily separating them from *tarsatus* and *williamsi*. Differences in geographic distribution aid in the identification of *tarsatus* and

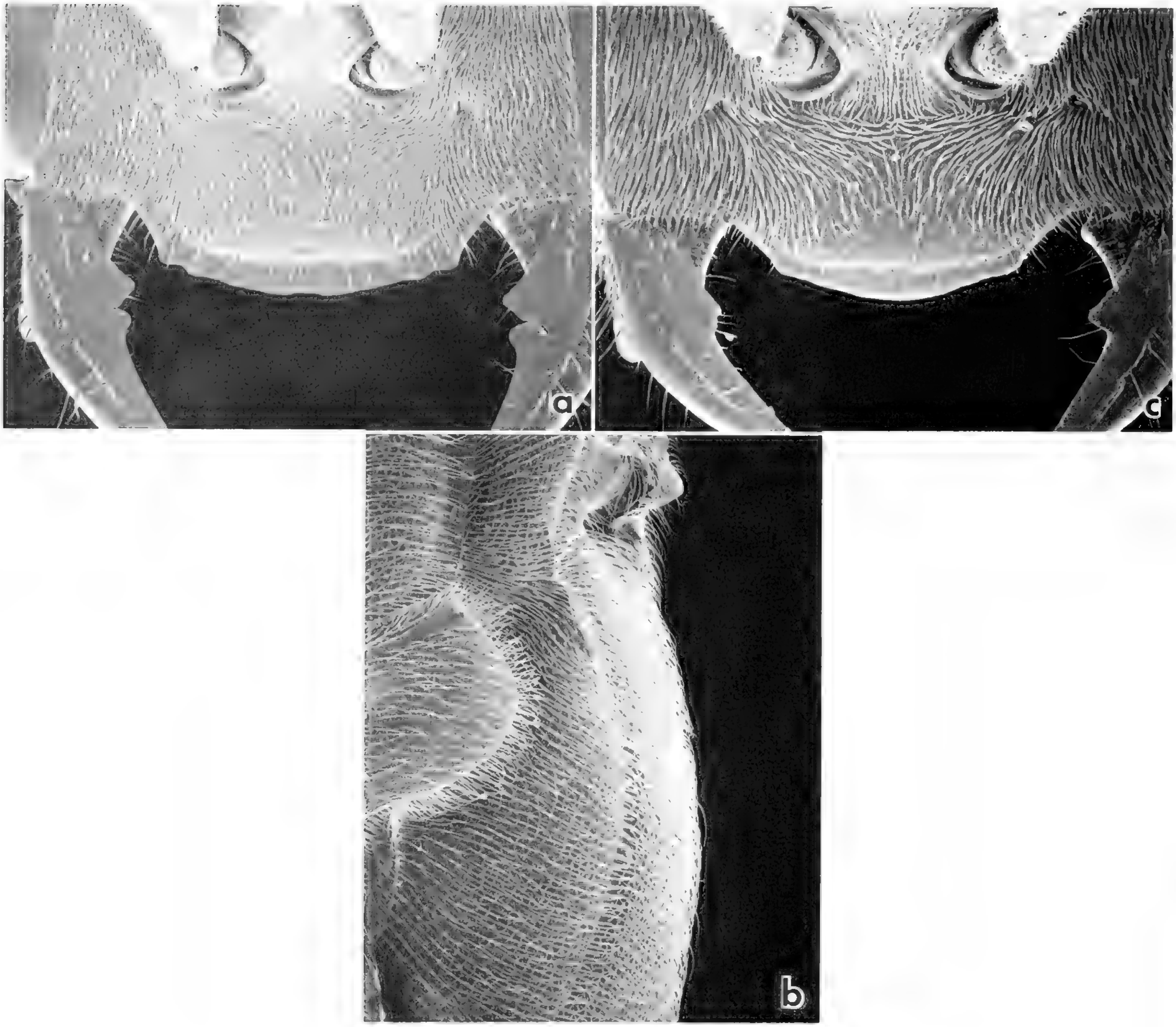

FIGURE 34. *Tachysphex tarsatus* (Say): a—female clypeus; b—female mesopleuron, front view; c—male clypeus.

williamsi. Both occur between the West Coast and the 100th meridian, but only *tarsatus* ranges between the 100th meridian and the East Coast and on the California Channel Islands (see also Discussion under *williamsi*).

The male of *tarsatus* has distinctive, suberect setae, about 1.0 MOD long, on sterna VI–VIII (Fig. 35a, b), and sinuous setae on the volsella and gonoforceps (Fig. 35c–g). In other species of the *pompiliformis* group, the sternal setae are appressed or nearly so (except in *williamsi* where they are erect, no longer than 0.4 MOD on sterna VI and VII), and the setae are straight on the volsella and gonoforceps.

DESCRIPTION.—Punctures shallow, subcontiguous on frons, less than to about one diameter apart on vertex, subcontiguous on scutum. Mesopleuron mat, granulose microrugose. Propodeal dorsum evenly microreticulate; side mat, finely ridged or uniformly microsculptured; hindface ridged, rarely uniformly microreticulate. Sternum I without apical depression. Micropunctures of tergum II two to three diameters apart. Hindcoxa not carinate.

Vestiture totally (male) or largely (female) obscuring sculpture between antennal socket and orbit. Vertex setae suberect, about 0.5 MOD long; scutal, mesopleural (Fig. 34b), and femoral setae appressed, but in occasional specimens subappressed just below subalar fossa.

Head, thorax, and legs black, tarsal apex reddish. Gaster red to black (see Variation below). Terga I–IV silvery fasciate apically. Wings moderately infumate to subhyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 34a): bevel shorter than basomedian area; the latter with usual dense punctation, and also with large, sparse, shallow punctures; lip arcuate, in most specimens incised laterally, very rarely with vestigial, mesal notch. Dorsal length of

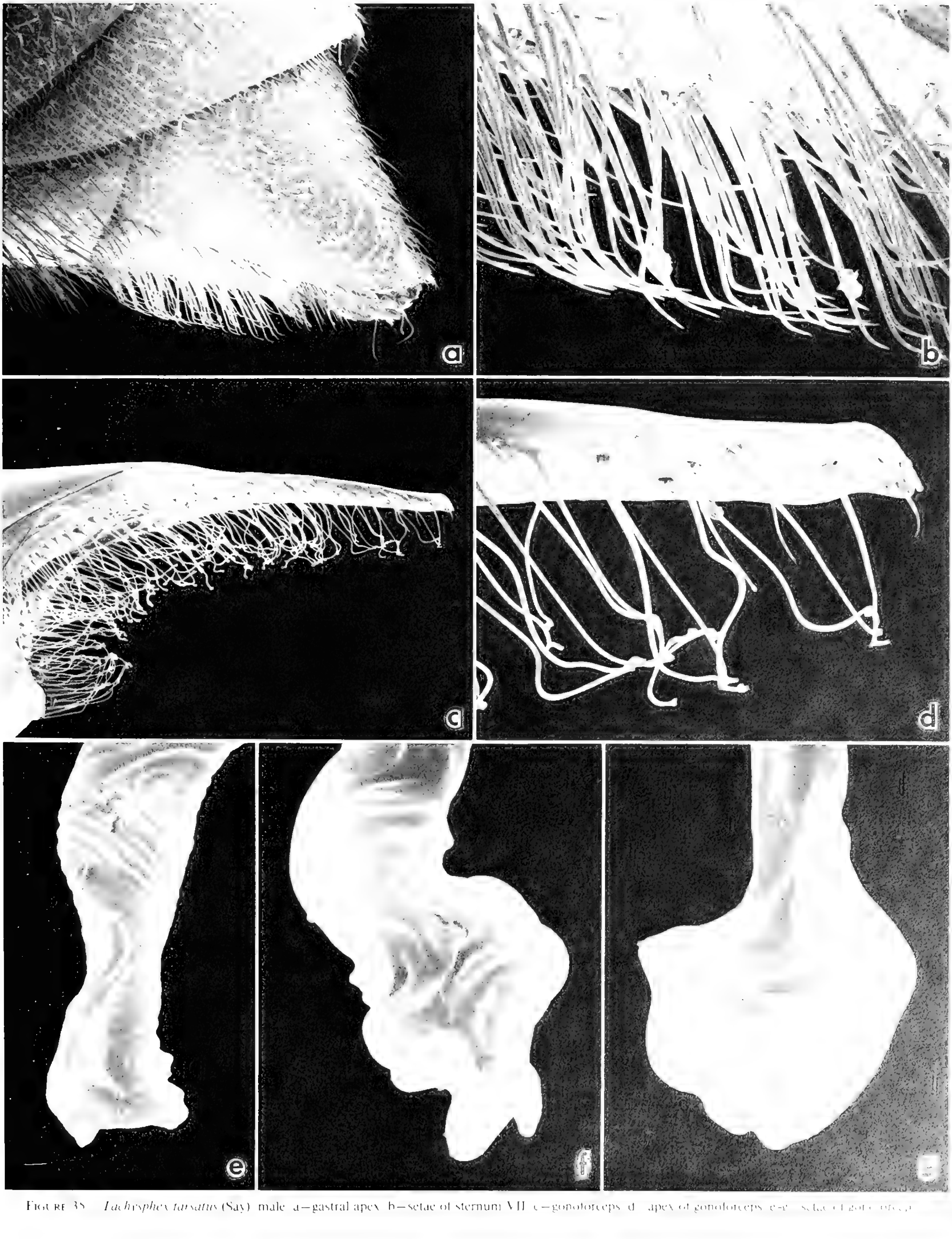

FIGURE 38. *Tachysphex tarsatus* (Say), male: a—gastral apex; b—setae of sternum VII; c—gonoforceps; d—apex of gonoforceps; e–g—setae of gonoforceps.

flagellomere I 2.0–2.5× apical width. Vertex as wide as long or slightly wider. Tergum V finely, densely punctate (somewhat sparsely in the middle), its apical depression impunctate. Pygidial plate shiny, punctate. Trochanteral and femoral punctation fine, dense. Length 6.5–10.0 mm.

♂.—Mandible with tooth on inner margin (Fig. 34c). Clypeus (Fig. 34c): bevel much shorter than basomedian area; lip arcuate, its corners obtuse, closer to orbit than to each other. Dorsal length of flagellomere I 1.3–1.7× apical width. Vertex width 1.3–1.6× length. Sterna densely punctate. Setae of apical sterna: Figure 35a, b. Forefemoral notch glabrous. Foretarsus with none to three preapical rake spines; outer apical spine of foretarsomere II shorter than foretarsomere III, but equal to this tarsomere length in one of the males from Tombstone area, Arizona. Length 5.5–7.0 mm. Gonoforceps and its setae: Figure 35c–g.

Sterna VI–VIII with dense, suberect setae whose length is about 1.0 MOD.

Variation.—The female gaster is red west of the 100th meridian, but tergum V and/or IV is darkened in many specimens from British Columbia and Alberta, and all gaster is black in specimens from Arcata (some specimens), Samoa, San Miguel Island, and San Nicolas Island, California, and Couperville and Friday Harbor, Washington. In most females the gaster is marked with black east of 100th meridian: tergum IV is black in most United States specimens, and terga IV and V are black in individuals from Ontario. However, the black covers terga IV–VI in certain specimens from Ontario, New England, Michigan, and North Carolina.

In most males, terga IV–VIII are black, but in some eastern specimens terga I–III also may be largely black. The gaster is all red in specimens from California, Oregon, Idaho, Arizona, and in many specimens from Utah and Colorado. It is black in a male from Andover, Massachusetts (MCZ), three males from Samoa dunes, California (UCD, UIM), all males examined from San Miguel Island and San Nicolas Island, California, a male from Florence, Oregon (OSU), and a male from Couperville, Washington (OSU).

Discussion.—The holotype (or syntypes) of *tarsatus* was lost (Fox 1902), and the original description is so inadequate that the species cannot be recognized with certainty. Therefore, I have followed the traditional interpretation of *tarsatus*. I have not designated a neotype, because suitable specimens from Arkansas were unavailable.

Life History.—Robertson (1928) found *tarsatus* on flowers of *Chamaecrista fasciculata* (Michx.) Greene (as *Cassia chamaecrista* (L.)) and *Cicuta maculata* L. Kurczewski (1966*b*) did not observe gregarious nesting, but I frequently saw aggregations of individuals. The nest is unicellular and permanently open during the provisioning period (Williams 1914; Evans 1970; Alcock and Gamboa 1975). The burrow is slightly inclined, at most 5 cm long, and the cell is 1–2.5 cm beneath the soil surface. Excavated soil forms a tumulus in front of the entrance. Peckham and Peckham (1900) observed orientation behavior (both walking and flying) after completion of a nest. The nest is provisioned with grasshoppers, in most cases *Melanoplus*, but also with Oedipodinae or Acridinae. Elliott and Kurczewski (1985: 293) report *Dissosteira carolina* (Linnaeus), *Melanoplus complanatipes* Scudder, *Orphulella pelidna* (Burmeister), and *Pseudopomala brachyptera* (Scudder), and Rust et al. (1985) report *Camnula pellucida* (Scudder). Most prey are nymphs, but the single individual of *Orphulella pelidna* was an adult. Riley (1880) reported that *tarsatus* preyed on the Rocky Mountain grasshopper, *Melanoplus spretus* (Walsh), but his wasp determination is dubious. Steiner (1981) established that four stings are used to paralyze the prey and described stinging sites on the prey's body. When carrying a prey, the female straddles it and holds its antennae with her mandibles (Williams 1914). His description suggests that the prey is kept venter up during transportation. Elliott and Kurczewski (1985:293) observed prey carrying females either walking on the ground or moving in a series of short flights. The prey may be brought directly into the burrow or (Williams 1914) first deposited at the entrance. In the latter case, the wasp enters the nest, turns around inside the nest, reappears headfirst, seizes the grasshopper by its antennae, and drags it backward into the burrow. The prey is deposited in the cell, venter up and head in, and the egg of the wasp is placed across the host's prosternum. The prey may be longer than the female or considerably smaller (in which case two prey per nest are supplied). Peckham and Peckham (1900) observed that the egg was not laid on the first prey brought in to the nest. To close the nest, the female gets up on the tumulus and backs several times into the entrance, pushing the earth in with her forelegs. She uses her pygidial area to tamp in the soil.

Williams (1914) also reported an unidentified sarcophagid fly that follows wasps carrying prey. These flies larviposit on the acridids deposited at the nest entrance.

Kurczewski (1966*b*) found that males usually frequent several perches, and occasionally one may chase another from a perch. They spend nights and inclement weather in burrows that are dug with their mandibles and forelegs. The burrows are closed from within and have no apical cell. Males stay at the end of their burrow, the head toward the entrance. During copulation (Kurczewski 1966*b*), the male mounts the female, and she spreads her wings laterally (at about 40–55° to the main axis of the body). In both cases observed by Kurczewski, the front legs of the male, probably the femora, appeared to hold the foremargin of the female wings (possibly with the forefemoral notches). The male's wings are folded flat over his dorsum during mating.

Geographic Distribution (Fig. 36).—Southern Canada to Georgia and Costa Rica; replaced by *laevifrons* in southeastern United States.

Material Examined.—1,403♀, 1,562♂, and also 720♀ which may be either *tarsatus* or *williamsi*.

Records.—CANADA: **Alberta:** Drumheller, 5 mi S Irvine, Lethbridge, Medicine Hat, Scandia. **British Columbia:** Okanagan Falls, Olivier, 4 mi S Princeton, Richter Pass Road (7 mi W Osoyoos), Robson, Summerland, Vernon. **Manitoba:** Aweme, Bald Head Hills (13 mi N Glenboro), Stockton. **Ontario:** Belleville, Brighton, Chatterton, Jordan, Merivale, Ottawa, Point Pelee. **Quebec:** Hull, Notre Dame du Portage. **Saskatchewan:** Christopher Lake, 10 mi W Moose Jaw, Prince Albert, Saskatoon, Swift Current, Willow Bunch.

UNITED STATES: ALABAMA: **Lee:** Auburn. ARIZONA: **Cochise. Coconino:** Flagstaff, Grand Canyon National Park. **Graham:** Roper Lake State Park. **Maricopa:** 3 mi SW Wickenburg. **Mohave:** 15 mi S Wikieup. **Navajo:** Jadito Trade Post, 16 mi SW Kayenta. **Pima:** Sahuarita, Santa Rita Mts., 10 mi SE Tucson. **Santa Cruz.** ARKANSAS: **Marion:** —. CALIFORNIA: **Alameda. Alpine. Butte:** 13 mi N Chico, Paradise. **Contra Costa. Del Norte:** Southern Fork of Smith River. **El Dorado. Fresno:** Fresno. **Humboldt. Inyo. Kern:** Antelope Canyon near Tehachapi, Cerro Noroeste (SW corner of county), Mill Potrero. **Lake:** Cobb. **Lassen. Los Angeles. Madera:** 11 mi N Fresno. **Marin. Mariposa:** El Portal, Mariposa. **Mendocino. Merced:** Dos Palos. **Modoc. Mono. Monterey. Napa. Nevada. Orange:** Fullerton, Santa Ana Canyon. **Placer. Plumas. Riverside. Sacramento:** Sacramento. **San Benito:** Idria (Gem Mine), Pinnacles National Monument. **San Bernardino:** Baldy Mesa, 1 mi W Cajon, 8 mi NE Cima, 2 mi W Phelan, Victorville. **San**

FIGURE 36. Geographic distribution of *Tachysphex laevifrons* (F. Smith) and *tarsatus* (Say).

Diego. **San Francisco:** San Francisco (Presidio Park). **San Joaquin:** Bacon Island, Stockton, Tracy. **San Luis Obispo. San Mateo:** Menlo Park, Redwood City. **Santa Barbara:** Bluff Camp, Goleta, Refugio Pass, San Miguel Island, Santa Cruz Island, Santa Rosa Island, Santa Ynez Mts. **Santa Clara:** Alum Rock Park, San Jose, Stanford University. **Santa Cruz:** Soquel. **Shasta. Sierra. Siskiyou. Solano:** Benicia State Recreation Area (3 mi SE Vallejo), Vallejo. **Sonoma:** Guernewood Park along Russian River. **Trinity:** Hayfork Ranger Station. **Tulare:** 8 mi NE Three Rivers. **Tuolumne. Ventura:** Foster Park, San Nicolas Island, Sespe, Wagon Road No. 2 Campground (18 air mi WSW Gorman). **Yolo:** Davis. COLORADO: **Alamosa:** Great Sand Dunes National Monument. **Bent:** Hasty. **Boulder. Chaffee:** Poncha Springs, Salida. **Clear Creek:** Mt. Evans (Doolittle Ranch), Oslar. **Costilla:** Ute Creek. **Custer:** Alvarado Creek (Sangre de Cristo Mts.). **Denver:** Denver. **Douglas:** 20 mi S Denver. **Eagle:** State Bridge. **Garfield:** Rifle. **Gilpin:** S Central City **Huerfano:** Gardner. **Jefferson:** Golden. **Larimer. Mesa:** 31 mi N Mack, Mesa area. **Moffat:** Craig, Dinosaur National Park. **Montezuma:** 3 mi W Arriola. **Pueblo:** Pueblo. **Rio Blanco:** 23 mi S Becker. **Rio Grande:** South Fork. **Teller:** Florissant **Weld:** Keenesburg, Owl Creek (12 mi NE Nunn), Roggen. CONNECTICUT: **Hartford:** E Hartford. **Middlesex:** Durham. **New Haven:** Bethany, 2 mi E Seymour. DELAWARE: **Sussex:** Lewes. DISTRICT OF COLUMBIA: Washington. GEORGIA: **De Kalb:** Stone Mountain (1♀, UGA). **White:** Cleveland (1♀, UGA). IDAHO: **Ada:** 10 mi S Boise. **Blaine:** 9 mi SW Bellevue, 2 mi W Carey (also 3 mi NW) **Bonneville:** 5 mi W Idaho Falls. **Butte:** Craters of the Moon National Monument **Camas:** 12 mi S Fairfield (also 23 mi E), 8 mi W Hill City. **Cassia:** 9 mi E Malta. **Clark:** Blue Dome. **Custer:** Lost River Mts , Salmon River (2 mi S Challis). **Elmore:** Dixie. **Franklin:** 5 mi NE Minkcreek, Preston, Thomas Springs. **Fremont:** Saint Anthony Sand Dunes. **Gooding:** 5 mi N Bliss, 1 mi N Gooding (also 12 mi N) **Idaho:** 10 mi NE Lowell. **Jefferson:** 3 mi N Terreton. **Kootenai:** 12 mi N Worley. **Latah:** Moscow. **Lincoln:** Shoshone (also 19 mi N). **Oneida:** Black Pine Canyon, 5 mi NW Holbrook, Twin Springs **Owyhee. Payette:** —. **Twin Falls:** Hollister. ILLINOIS. Chicago. **Champaign:** Urbana. **McHenry:** Algonquin. **Kane:** near Camp Big Timber. **Lake:** Lake Forest. **Mason:** Bath, Havana (Devils Neck), Sand Ridge State Forest. **Whiteside:** Fulton. IOWA: **Jackson:** Bellevue. **Woodbury:** Sergeant Bluff, Sioux City. KANSAS. **Clay:** Clay Center. **Gray:** Cimarron. **Pottawatomie:** Blackjack Creek. Also **Barton, Grant, Hamilton, Meade, Morton, Ness, Norton, Osborne, Phillips, Rooks, Rush, Trego:** —. MAINE: **York:** 4 mi SW Kennebunk, Limington. MARYLAND: **Prince Georges:** Beltsville. MASSACHUSETTS: Boston. **Barnstable:** Provincetown, Sagamore, Wellfleet. **Dukes:** Nonamesset Island **Essex:** Andover, Lynn. **Hampden:** Holyoke. **Hampshire:** Southampton. **Middlesex:** Bedford, Lexington **Norfolk:** Needham, Wellesley. **Plymouth:** Manomet MICHIGAN: **Alger:** Pictured Rocks National Lakeshore. **Benzie:** —. **Cheboygan:** Cheboygan, Douglas Lake **Clinton:** Rose Lake. **Delta. Isabella. Leelanau:** — **Livingston:** E. S George Reserve. **Marquette:** Huron Mountain Club, Marquette **Midland:** —. **Muskegon:** Muskegon County Park. **Oceana:** Claybank Township Park **Ogemaw:** —. **St. Joseph:** Mohney Lake. **Washtenaw:** Pinckney State Recreation Area near Half Moon Lake. MISSISSIPPI: **Lafayette:** Oxford. MISSOURI: **Boone:** Columbia. MONTANA: **Beaverhead:** 3 mi W Jackson. **Dawson:** Glendive **Lewis and Clark:** Helena. **Ravalli:** Hamilton (Rocky Mountain Laboratory). **Rosebud:** Ashland **Sanders:** Dixon **Sweet Grass, Teton:** — NEBRASKA: **Blaine:** 5 mi N Chinook, Dunning, Halsey. **Cherry:** 10 mi N Nenzel (on Niobrara River), Valentine. **Cuming:** West Point. **Dawes:** Chadron. **Douglas:** Omaha. **Hooker:** 1.5 mi N Mullen **Keith:** Ogallala. **Lincoln:** North Platte, Wallace. **Nance:** Genoa **Scotts Bluff:** 8 mi S Gering, Mitchell **Sheridan:** Bingham, Rushville. **Sioux:** Glen, Monroe Canyon, Sawbelly, Toadstool Park (18 mi N Crawford). **Thomas:** Thedford NEVADA. **Douglas:** 4 mi NE Glenbrook, Minden. **Elko. Esmeralda:** Walker Springs. **Eureka:** 1 mi W Emigrant Pass, 14 mi W Eureka. **Humboldt:** Canyon Creek, Orovada **Lincoln:** Highland Range near Mendha. **Lyon:** Sweetwater. **Mineral:** 4 5 mi S Schurz **Nye. Washoe. White Pine:** Charcoal Oven State Park, 10 mi NW Preston NEW HAMPSHIRE: **Belknap:** Lake Winnipesaukee. **Rockingham:** Hampton, Salem NEW JERSEY: **Bergen:** Closter. **Burlington:** Browns Mills, Lebanon State Forest, Riverton **Camden:** Atco, Clementon. **Cape May:** Reeds Beach, Sea Isle City **Gloucester:** —. **Mercer:** Princeton. **Monmouth:** Little Silver, Ocean Township, Tinton Falls. **Ocean:** Lakehurst, Point Pleasant. NEW MEXICO. **Bernalillo:** Albuquerque. **Catron:** Pie Town. **Colfax:** 2 mi N Ute Park. **Dona Ana:** 5 mi E Las Cruces. **Grant:** 1 mi S Silver City. **Hidalgo:** 15 and 21 mi S Animas, Rodeo (also 7 mi SE) **Lincoln:** Alto **Otero:** Alamogordo. **Quay:** Tucumcari **Roosevelt:** Oasis State Park. **San Juan:** Newcomb. **San Miguel:** Las Vegas **Sierra:** Percha Dam State Park **Socorro:** La Joya (20 mi N Socorro), 16 mi W Magdalena, 37 mi S Socorro **Torrance:** Tajique **Valencia:** 3 mi E Laguna. NEW YORK **Albany. Cayuga:** Auburn, Fair Haven **Erie:** Buffalo. **Fulton:** Broadalbin **Jefferson:** road 37 W Theresa. **Madison:** Chittenango. **Monroe:** Irondequoit, Mendon Ponds, Rochester **Nassau:** Long Beach, North Bellmore. **Oswego:** Granby Center, Mallory, Oswego **Otsego:** Cooperstown. **Saint Lawrence:** Wanakena. **Saratoga:** Middle Grove **Schoharie:** Schoharie. **Suffolk:** Bohemia, Cold Spring Harbor, Coram Farmingville, Orient, Smithtown **Tompkins. Warren:** Pottersville **Wayne:** —. **Westchester:** Peekskill. NORTH CAROLINA: **Dare:** Kill Devil Hills, Nags Head, S Salvo. **Moore:** Southern Pines. **Onslow:** Jacksonville. NORTH DAKOTA: **Bowman:** Bowman. **Golden Valley:** Beach. **Hettinger:** Mott. **McHenry:** Towner. **Stark:** Dickinson. OKLAHOMA: **Woods:** 3 mi W Waynoka. OREGON: **Harney:** Frenchglen, Steen Mts. **Jackson:** Gold Hill, Medford. **Klamath:** Klamath Falls. **Lake:** Chowaucan River. **Lane:** 2 mi S Florence. **Sherman:** Rufus. **Washington:** Cornelius. PENNSYLVANIA: **Bradford:** Wilawana. **Erie:** Erie, Presque Isle State Park. **Montgomery, Pike:** —. RHODE ISLAND: **Newport:** Newport. SOUTH DAKOTA: **Custer:** Black Hill National Forest. TENNESSEE: **Morgan:** Burrville. TEXAS: **Hudspeth:** McNary. **Jeff Davis:** 11 mi NE Fort Davis. **Randall:** Palo Duro Canyon State Park. UTAH: **Box Elder. Cache. Davis:** Farmington. **Duchesne:** Duchesne. **Emery:** N Goblin Valley (Buckskin Spring, Orange Olsen Ranger Station, Wild Horse Creek). **Garfield:** Calf Creek, 24 mi N Panguitch. **Grand:** Capital Reef National Park, Castleton. **Juab:** 5 mi W Callao. **Millard:** Delta, 12 mi N Fillmore, Gandy. **Rich:** Bear Lake. **San Juan:** Kane Springs (E Bridges National Park), 25 mi S Moab. **Summit:** Snyderville. **Tooele:** Simpson Spring, Tooele. **Uintah:** 17 mi S Bonanza. **Utah:** Spanish Fork. **Washington:** Leeds Canyon, Zion National Park. **Wayne:** Grover, Hanksville, Torrey. **Weber:** Eden, Willard Basin. VERMONT: **Caledonia:** W Danville. **Essex:** —. **Orange:** Thetford, Union Village. VIRGINIA: **Fairfax:** Barcraft, Falls Church. **Norfolk:** Norfolk. WASHINGTON: **Adams:** 7 mi N Othello. **Asotin:** Field Springs State Park. **Clark:** Vancouver. **Franklin:** Richland. **Garfield:** Central Ferry. **Grant:** O'Sullivan Dam. **Island:** Coupville. **Lincoln:** Odessa. **San Juan:** San Juan. **Spokane:** Mead. **Whitman:** Pullman, Wawawai (also 2 mi E). **Yakima:** Yakima. WEST VIRGINIA: **Wirt:** —. WISCONSIN: **Milwaukee:** Milwaukee. **Walworth, Washington:** —. WYOMING: **Albany:** Laramie, Summit. **Big Horn:** 10 mi E Shell. **Carbon:** Rawlins. **Converse:** Glenrock. **Fremont:** Riverton. **Goshen:** Torrington. **Lincoln:** Etna. **Natrona:** Pathfinder Dam (8 air mi SW Alcova). **Niobrara:** —. **Park:** Powell. **Sweetwater:** 20 mi E Farson, Green River (also 15 mi S). **Teton:** 5 mi S Elk Post Office, Hoback Junction, Jackson Hole

MEXICO: **Baja California Norte:** S Coronado Island, Descanso, 10 mi S San Quintin, Santo Domingo area, San Vicente. **Chihuahua:** 35 mi N Chihuahua, Mesa del Huracán (30°04'N, 108°15'W). **Distrito Federal:** Porto de las Cruces. **Durango:** Rodeo. **Hidalgo:** 5 mi W Pachuca. **Jalisco:** Guadalajara, 8 km E Ojuelos. **México:** Tepexpan. **Puebla:** 14 mi W Huachinango. **Querétaro:** Palmillas. **Sinaloa:** 8 mi SE Elota. **Sonora:** Alamos, E Yaqui River (35 air km WSW Sahuaripa). **Zacatecas:** 2 km SW Valparaiso

COSTA RICA: **San Jose:** San Antonio de Escazu

Tachysphex williamsi R. Bohart

(Figures 37, 38)

Tachysphex williamsi R. Bohart, 1962:38, ♀, ♂. ! Holotype: ♂. California: San Francisco: Lone Mt. (CAS).—Krombein 1967:394, Bohart and Menke 1976: 277; Krombein 1979:1630; Elliott and Kurczewski 1985:294.

Diagnosis.—The female of *williamsi* cannot be distinguished from *tarsatus*, but details of geographic distribution help in identification (see *tarsatus* for more information). The male has distinctive straight setae on sterna VI–VIII, up to 0.4 MOD long (Fig. 37), and setae on the volsella and gonoforceps are straight also. In *tarsatus*, the sternal setae are curved apically, about as long as MOD, and those on the gonoforceps and volsella are sinuate, thickened apically.

Description.—Punctures subcontiguous on frons, vertex, and scutum. Frontal punctures shallow. Mesopleuron mat, microrugose, or with shallow, inconspicuous punctures. Propodeal dorsum evenly microareolate; side opaque, uniformly microsculptured or finely, irregularly ridged; hindface ridged, but almost uniformly microsculptured in occasional specimens. Sternum I without apical depression. Discal micropunctures of tergum II one to three diameters apart. Hindcoxa not carinate.

Setae appressed on vertex or (some specimens) erect, about 1.0 MOD long; appressed on scutum, mesopleuron, and femora.

Head, thorax, and legs black, tarsal apex sometimes reddish. Gaster red or black. Wings subhyaline to infumate. Terga I–III (female) or I–IV (male) silvery fasciate apically.

♀.—Clypeus: bevel shorter than basomedian area; the latter with usual, dense punctation, and also with large, sparse, shallow

punctures; lip arcuate, indented laterally. Dorsal length of flagellomere I 1.8–2.3× apical width. Vertex as wide as long or slightly wider. Tergum V sparsely punctate mesally, its apical depression impunctate. Pygidial plate shiny, punctate. Trochanteral and femoral punctation fine, dense, but mid- and hindtrochanteral venter often sparsely punctate. Length 8–10 mm.

Integument not obscured by vestiture between antennal socket and orbit.

♂.—Mandibular inner margin with tooth. Clypeus: bevel much shorter than basomedian area; lip arcuate, its corners rectangular or obtuse, closer to orbit than to each other. Dorsal length of flagellomere I 1.4–1.6× apical width. Vertex width 1.3–1.6× length. Sterna densely punctate. Sternal setae: Figure 37. Forefemoral notch glabrous. Forebasitarsus with none to three preapical rake spines; outer apical spine of foretarsomere II shorter than foretarsomere III. Length 5.5–8.0 mm.

Integument totally hidden under vestiture between antennal socket and orbit. Sterna I–VI with very short, appressed pubescence; setae of sternum VII and VIII up to 0.4 MOD long.

VARIATION.—Setae of male sternum VII and VIII varying from very short, nearly appressed, to erect, about 0.4 MOD long. Both extremes may occur within the same population, e.g., in specimens from San Francisco (Lobos Creek, Laguna Puerca).

The gaster is red with black apex in most specimens, but all black in many specimens from California (especially from the coast). In a series from Hasty, Colorado, the gaster is all red in most specimens but all black in some males.

DISCUSSION.—Females of *tarsatus* and *williamsi* seem identical, but males can be separated by abdominal features: the shape and length of setae on sterna VI–VIII, and on the gonoforceps and volsella. R. Bohart (1962) thought that the two species differed in gaster color (all or partly red in *tarsatus*, all black in *williamsi*), but actually both species vary from all red to all black. *Tachysphex tarsatus* is transcontinental and also occurs on the Channel Islands, California, while *williamsi* ranges between the West Coast and the 100th meridian. The status of *tarsatus* and *williamsi* can be interpreted two ways:

1) Both are good species whose females do not differ morphologically. The sternal and genital setae in the male of *tarsatus* are unique within the genus, and no intergradation with *williamsi* has been found.

2) *Tachysphex tarsatus* and *williamsi* represent a single species in which males are dimorphic west of the 100th meridian. Between the West Coast and the 100th meridian males of both types occur together in most localities. However, there are instances where only one type of male occurs (*tarsatus* on the California Channel Islands, *williamsi* in some coastal habitats of central California, e.g., in San Francisco and Marin County). Because of this I have concluded that the first hypothesis is more probable, and I regard *williamsi* as distinct from *tarsatus*.

LIFE HISTORY.—Elliott and Kurczewski (1985:294) recorded a nymph of the acridid *Trimerotropis occidentalis* (Bruner) as prey.

GEOGRAPHIC DISTRIBUTION (Fig. 38).—Rocky Mountains to the West Coast, south to Baja California Norte; also Saskatchewan, Alberta, and North Dakota.

MATERIAL EXAMINED.—54♀, 217♂ (see also figures under *tarsatus*).

RECORDS (b: gaster all black).—CANADA: **Alberta:** Coaldale, Dunmore, Writing-on-Stone Provincial Park. **Saskatchewan:** Regina.

UNITED STATES: ARIZONA: **Cochise:** 5 mi W Portal. CALIFORNIA: **Amador:** Hams Station. **Contra Costa:** Mt. Diablo. **Inyo:** 12 mi E Big Pine. **Lassen:** Hallelujah Junction. **Marin:** Carson Ridge (b), Dillon Beach (b), Point Reyes (b). **Monterey:** Fort Ord. **Nevada:** Prosser Dam. **San Bernardino:** Big Bear Lake, Dollar Lake trail, Holcomb. **San Diego:** Mt. Laguna, Pine Valley, Warner Springs. **San Francisco** (all b except some females from Laguna Puerca partly red): San Francisco (Baker Beach, Ingleside, Laguna Puerca, Lake Merced, Land's End, Lobos Creek, Lone Mt., Presidio Park). **San Mateo:** San Bruno Mts. (b). **Siskiyou:** Macdoel **Sutter:** Nicolaus (b). COLORADO: **Bent:** Hasty (partly b). **Boulder:** Boulder, Hygiene. **Chaffee:** Buena Vista. **Costilla:** Ute Creek (b). **Denver:** 20 mi S Denver. **El Paso:** Colorado Springs. **Kit Karson:** Flagler. **Larimer:** Chimney Rock (60 mi NW Fort Collins, 8,000 ft), Poudre Canyon. **Teller:** Florissant. IDAHO: **Blaine:** 2 mi W Carey. **Butte:** 6 mi S Howe. **Camas:** 23 mi E Fairfield. **Cassia:** 2.5 mi S Malta (also 9 mi E). **Elmore:** Mayfield. **Fremont:** Saint Anthony Sand Dunes. **Gooding:** 1 mi NE Gooding, Hagerman Valley. **Jefferson:** 6 mi N Roberts. **Lincoln:** Dietrich Butte (also 5 mi E), Shoshone. **Oneida:** 5 mi S Holbrook. **Twin Falls:** Castleford, Hollister, Rogerson, Roseworth. MONTANA: **Dawson:** Glendive. **Stillwater:** —. NEBRASKA: **Dawes:** Chadron. **McPherson:** Sandhills. NEVADA: **Elko:** Tuscarora. **Washoe:** 1 mi S Mustang, 15 mi E Reno. **White Pine:** 16 mi S Ely, Lehman Cave. NEW MEXICO: **Catron:** Pie Town. NORTH DAKOTA: **Bowman:** Bowman, Gascoyne. OREGON: **Malheur:** 3 mi S Vale. UTAH: **Box Elder:** Snowville, 12 mi W Tremonton. **Cache:** Cornish. **Uintah:** SW Bonanza. WASHINGTON **Garfield:** Central Ferry. **Grant:** Sullivan Dam. WYOMING: **Albany:** Laramie. **Big Horn:** Lovell. **Carbon:** Rawlins. **Sweetwater:** Little America

MEXICO: **Baja California Norte:** El Progreso

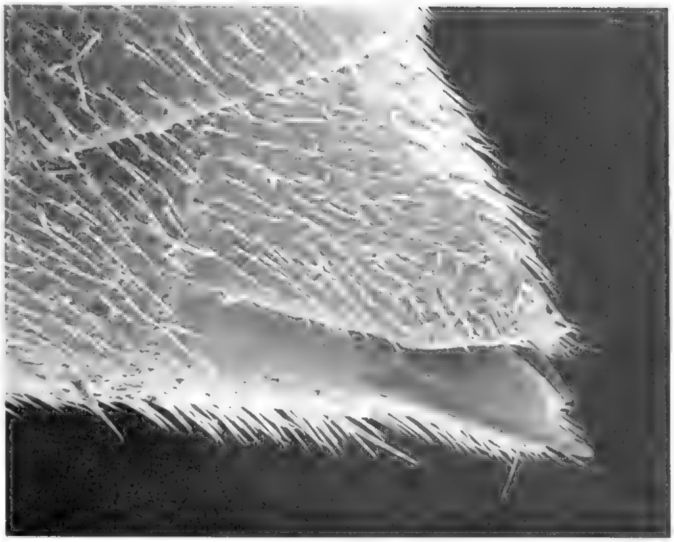

FIGURE 37. *Tachysphex williamsi* R. Bohart: gastral apex of male.

Tachysphex spatulifer Pulawski

(Figures 39, 40)

Tachysphex spatulifer Pulawski, 1982:35, ♀, ♂. ! Holotype: ♀, California: Monterey Co.: Arroyo Seco Camp (UCD)

DIAGNOSIS.—*Tachysphex spatulifer* is very similar to *crenulatus*. See the latter species for recognition characters (page 65).

DESCRIPTION.—Punctures less than one diameter apart on frons, scutum, mesothoracic venter, and trochanters. Vertex wider than long. Mesopleuron dull, roughly microsculptured, impunctate. Propodeal dorsum microareolate; side and hindface ridged or (some specimens) microridged. Sternum I without apical depression. Hindcoxa not carinate.

Vestiture totally obscuring integument between antennal socket and orbit. Setae appressed on vertex, scutum, and femora, suberect on hypoepimeral area, subappressed or (some females) suberect below mesopleural scrobe, oriented almost evenly posterad on scutal disk.

FIGURE 38. Geographic distribution of *Tachysphex williamsi*

Head, thorax, and legs black, tarsal apex reddish. Wings weakly infumate. Terga I–III indistinctly, silvery fasciate apically (fasciae interrupted mesally).

♀.—Clypeus (Fig. 39a, b): bevel shorter than basomedian area, but sparsely punctate portion of middle section usually longer than densely punctate portion; lip broadened mesally, with one lateral incision, usually variably obtusely dentate (including one median tooth), but sometimes obtusely angulate; lip surface with several shallow, longitudinal, ill-defined furrows. Dorsal length of flagellomere I 2.3–2.7× apical width. Vertex punctures averaging from less than one to about two diameters apart. Tergum V densely or sparsely punctate at middle, its apical depression impunctate. Length 8.0–10.5 mm.

Gaster red. Frontal vestiture silvery or with golden tinge.

♂.—Inner mandibular margin not dentate (Fig. 39c). Clypeus (Fig. 39c): bevel ill defined; free margin very obtusely angulate between lobe and lateral section, apex of angle represented by small tubercle; tubercles usually slightly closer to orbits than to each other (but closer to each other in some specimens); lip obtusely triangular. Dorsal length of flagellomere I 1.4–1.7× apical width. Vertex width 1.2–1.4× length. Vertex punctures no more than one diameter apart. Discal micropunctures of tergum II one diameter apart or less. Sterna finely, evenly punctate, punctures well defined. Forefemoral notch glabrous. Foretarsus without rake; outer apical spine of foretarsomere II shorter than foretarsomere III. Length 5.5–8.0 mm.

Gaster usually bicolored (segments I–II or I–III red, remainder black), but all red in a male from Arroyo Seco, California (UCD) and another from Elba–Basin Pass (UIM). Frontal vestiture golden.

VARIATION.—Gena mostly thick in dorsal view, but thin in a female from Pinyon Flat.

Several males differ in having silvery frontal vestiture, and also:

1) Gena thin in dorsal view, gaster all red. California: Los Angeles Co.: Tanbark Flat, R. C. Bechtel (1♂, UCD); San Bernardino Co.: 10 mi N Lake Arrowhead, P. E. Paige (1♂, UCD), Cajon Junction, E. I. Schlinger (1♂, UCD).

2) Clypeal lip acutely angulate, lip corners slightly closer to each other than to orbits; gaster all red or with black apex. Utah: Weber Co.: Willard Peak, G. Bohart and P. Torchio (2♂, UCD).

These phena may be varieties of *spatulifer* or separate species. Study of topotypical females should solve this problem.

GEOGRAPHIC DISTRIBUTION (Fig. 40).—Washington to California and southwestern Arizona, eastward to southern Idaho and northern Utah.

MATERIAL EXAMINED.—84♀, 140♂ (CAS, CIS, CSDA, FCDA, MCZ, SDNH, TLG, UCD, UCR, UIM, USNM, USU)

RECORDS.—UNITED STATES: ARIZONA: **Yuma:** Colorado City. CALIFORNIA: **Alameda:** Arroyo Mocho (17 mi S Livermore), 1 mi E Mission Peak, Sycamore Grove State Park. **Amador:** Plymouth, Volcano. **Contra Costa:** Las Trampas Ridge (W Danville), Moraga, Mt. Diablo. **El Dorado:** Placerville. **Fresno:** Deer Cove Creek (12 air mi E Hume), Fresno, Warthan Canyon, Watts Valley. **Kern:** Glennville, Tejon Canyon, 1 mi E Woody. **Lake:** Borax Lake near Clearlake Park, N Fork Cache Creek at Highway 20. **Madera:** Buck Camp in Yosemite National Park. **Mariposa:** El Portal, Indian Flat. **Mendocino:** 5 mi N Branscomb, Mendocino. **Monterey:** Arroyo Seco Camp, 5 mi S Jamesburg, Monterey. **Napa:** Samuel Springs (now bottom of Lake Berryessa). **Placer:** 4 mi S Rocklin. **Riverside:** Pinyon Flat (San Jacinto Mts.). **Sacramento:** Folsom (also 10 mi NE), N Sacramento. **San Diego:** La Mesa, Sorrento. **San Luis Obispo:** 2.5 mi Creston, La Panza Camp (12 mi NE Pozo), Pozo (also 3 mi E), 5 mi E Santa Margarita. **Santa Clara:** Los Gatos, Mt. Hamilton. **Sierra:** Independence Lake. **Siskiyou:** Dry Lake Mountain (7 mi NNW town of Klamath River), Windy Camp. **Solano:** Mix Canyon, Pleasants Valley road 5 mi S Highway 128, Vacaville. **Sonoma:** Pepperwood Ranch Natural Reserve (10 mi N Santa Rosa). **Stanislaus:** 3.2 mi W Hwy. 120 on Evergreen Road. **Tulare:** Ash Mt., Camp Wishon (8 air mi NE Springville), Fountain Springs, Porterville, Sequoia National Park, Tule River Indian Reservation, Woodlake.

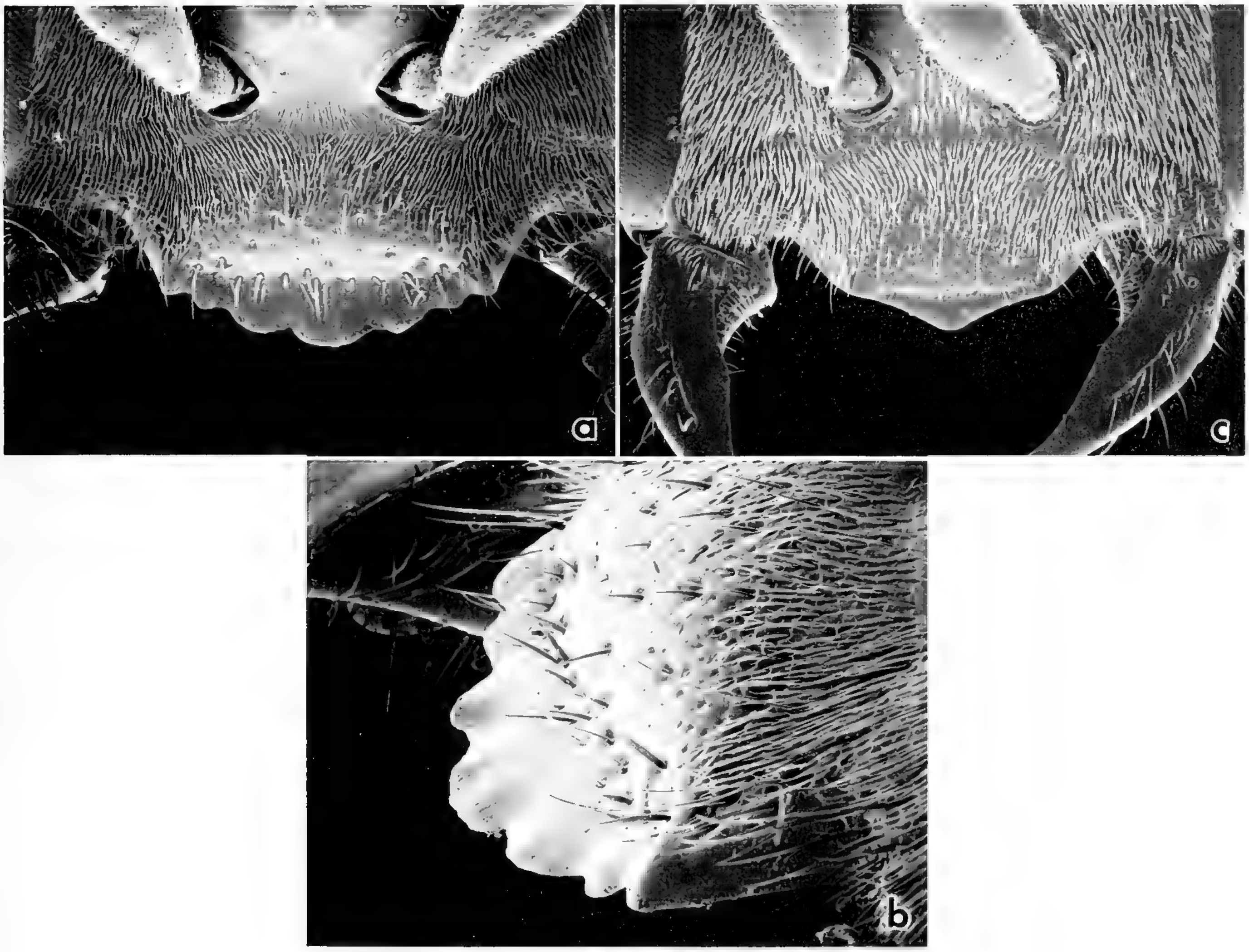

Figure 39. *Tachysphex spatulifer* Pulawski: a—female clypeus; b—female clypeus, oblique view; c—male clypeus.

Tuolumne: Buck Meadows, Mather, 4 mi E Sonora. **Ventura:** Hungry Valley (5 mi S Gorman). **Yolo:** Bear and Cache Creeks junction, Davis, Putah Canyon, Rumsey. IDAHO: **Ada:** Boise. **Cassia:** Elba–Basin Pass. **Fremont:** Saint Anthony Sand Dunes. **Oneida:** Black Pine Canyon. **Washington:** 2 mi N Mann's Creek. NEVADA: **Storey** (formerly Ormsby): Carson City area. OREGON: **Umatilla:** Athena. UTAH: **Cache:** W Hodges Canyon, White Pine Lake near Logan. **Weber:** Willard Peak. WASHINGTON: **Pacific:** Nahcotta.

Tachysphex crenulatus W. Fox

(Figures 41, 42)

Tachysphex crenulatus W. Fox, 1894*a*:512, ♀, ! Holotype: ♀, California: no specific locality (ANSP).—Dalla Torre 1897:679; Cresson 1928:44; G. Bohart 1951: 950; Bohart and Menke 1976:273; Krombein 1979:1628.

Diagnosis.—*Tachysphex crenulatus* has an impunctate, uniformly microsculptured mesopleuron. In the female, the clypeal lip has several shallow concavities (Fig. 41b), the lip margin is variously dentate or undulate (Fig. 41a), in most specimens emarginate mesally, and the mid- and hindfemoral venter is sparsely punctate. A similar clypeus is also found in *spatulifer* (in which the clypeal lip has a median projection or is obtusely broadened mesally, and the trochanteral venter is densely punctate), and in *musciventris* (which has a distinctive mesothoracic venter). The male of *crenulatus* has a triangular clypeal lip (Fig. 41c), the midscutal setae are oriented uniformly posterad, and the sterna are uniformly punctured, with nonvelvety pubescence. It is very similar to *spatulifer* and can be separated from that species only with difficulty. However, the trochanteral punctation helps in identification. Punctures are uniformly subcontiguous in *spatulifer*, but more than one diameter apart on the midtrochanteral venter anteriorly in most *crenulatus* (also on hindtrochanter in many specimens). Furthermore, the lip corners of *crenulatus* are closer to each other than to the orbits, and the frontal vestiture is silvery. In most *spatulifer*, the lip corners are closer to the orbits than to each other, and the frontal vestiture is golden (but see Variation under that species).

Description.—Frontal punctures fine, subcontiguous. Punctures no more than one diameter apart on vertex and scutum. Mesopleuron impunctate, microsculptured. Propodeal dorsum evenly microareolate; side and hindface coriaceous or microridged, but side finely ridged in some males. Hindcoxa not carinate or (some females) carinate only basally.

Setae appressed on scutum and femora, suberect on hypo-

FIGURE 40. Geographic distribution of *Tachysphex spatulifer* Pulawski.

epimeral area, subappressed beneath mesopleural scrobe, oriented evenly posterad on scutum at middle.

Head, thorax, and legs black, or hindfemur (some females) and hindtibia (some males) partly red; tarsal apex reddish. Gaster all red, or (some females) with irregular, black spots, or (a male from Phoenix, Arizona) gastral apex black.

♀.—Clypeus (Fig. 41a, b): bevel longer than basomedian area; lip margin in most specimens with one lateral and one sublateral incision and with mesal notch that is flanked by an obtuse tooth on each side; free margin undulate in specimens in which incisions are absent; lip surface with several shallow, ill-defined concavities. Dorsal length of flagellomere I 2.2–2.6 × apical width. Vertex as wide as long or wider. Discal micropunctures of tergum II at least one to two diameters apart, of tergum III two to five diameters apart. Tergum V with a few, scattered punctures, its apical depression impunctate. Pygidial plate smooth or alutaceous, sparsely punctate. Mid- and hindtrochanteral venter sparsely punctate, shiny. Forefemoral venter with minute, subcontiguous punctures. Length 8–10 mm.

Integument not concealed by vestiture between antennal socket and orbit. Vertex setae appressed, suberect anteriorly, 0.3–0.5 MOD long.

Terga II–IV silvery fasciate apicolaterally (but fasciae evanescent in many specimens). Wings moderately infumate.

♂.—Mandibular inner margin not dentate (Fig. 41c). Clypeus (Fig. 41c): bevel indistinctly delimited from both lip and basomedian area, but shorter than the latter; lip roundly triangular to sharply prominent, side of prominence concave (lip corners pointed) or straight (most small specimens); in the latter case free margin not angulate between lobe and lateral clypeal section (lip corners inconspicuous); lip corners closer to each other than to orbits. Dorsal length of flagellomere I 1.2–1.7 × apical width. Vertex width 1.3–1.4 × length. Discal micropunctures of tergum II two to three diameters apart to (some specimens) one diameter apart. Sternal punctures fine, dense to (some specimens) sparse, apical depression of sterna II–VI occasionally impunctate. Forefemoral notch almost glabrous. Punctures of midtrochanteral venter anteriorly several to many diameters apart in most specimens, but one diameter or less apart in some individuals (extreme variants can be observed within a single population, e.g., in specimens from Yavapai Co., Arizona). Foretarsus without rake, but outer apical spine of foretarsomeres I and II in some specimens longer than width of these tarsomeres. Length 7–9 mm.

Vestiture partly hiding integument between antennal socket and orbit. Vertex setae erect, 0.8 MOD long, or appressed posteriorly and subappressed anteriorly, 0.6 MOD long.

Hindtibia largely red in two California specimens examined (UCD): from Short Canyon, Kern Co., and Tanbark Flat, Los Angeles Co. Terga II–IV (sometimes I–V) silvery fasciate apically, but fasciae interrupted mesally. Wings almost hyaline to weakly infumate.

LIFE HISTORY.—Two females examined (UCD) are pinned with prey acridids: one from Arroyo Seco, California with *Melanoplus marginatus* (Scudder), and one from Aztec, Arizona with *Trimerotropis* sp. (determinations by D. C. F. Rentz).

GEOGRAPHIC DISTRIBUTION (Fig. 42).—California, Nevada, to southern Colorado and southern New Mexico, also northern Baja California.

MATERIAL EXAMINED.—134♂, 214♀.

RECORDS.—UNITED STATES. ARIZONA: **Cochise:** Portal, 16 mi N Willcox. **Maricopa:** 8 mi S Buckeye, Gila Bend (also 12, 27, and 32 mi E), Phoenix, Rainbow valley, 15 mi SE Wickenburg, route 74 5 mi W route 17. **Mohave:** 5 mi N Kingman (also 15 mi W), Oatman, 17 mi SE Topock, Wikieup (also 24 mi SE). **Pima:** 10

FIGURE 41. *Tachysphex crenulatus* W. Fox: a—female clypeus; b—clypeal lobe of female, oblique view; c—male of clypeus.

mi N Ajo, Sabino Canyon, Silver Bell, Tucson. **Pinal:** 9 mi N Florence, Picacho Pass. **Yavapai:** 8 mi N Aguila. **Yuma:** Aztec, 20 mi E Dateland, 7, 9, 14, and 32 mi S Quartzsite, 20 mi E Roll. CALIFORNIA: **Alameda:** Tesla Road. **Fresno:** Coalinga (also 10 mi W, 14 mi NE), Jacalitos Canyon (6 mi S Coalinga). **Kern:** 18 mi E Bakersfield, California City, Cuyama Valley, Glennville, Grapevine, McKittrick, Mill Potrero (18 mi SE Maricopa), 7 mi NW Mojave, Randsburg, Short Canyon. **Kings:** Avenal, Milham City. **Los Angeles:** 15 mi E Gorman, 5 mi S Lancaster, 8 mi N Llano, Palmdale, Tanbark Flat. **Madera:** Oakhurst. **Marin:** Alpine Lake. **Monterey:** Arroyo Seco, Monterey, 1 mi S Soledad, Stone Canyon (ca. 14 mi SW Coalinga). **Riverside:** Aguangua, Banning, Black Mountain, 18 mi W Blythe, Cabazon, Calimesa, Diamond Valley (3 mi S Hemet), Hemet Reservoir and Herkey Creek in San Jacinto Mts., Millard Canyon, Springs, Pinyon Flat (10 road mi SW Palm Desert), Riverside, Sage (also 5 mi S), Thousand Palms, Whitewater near Palm Springs. **San Benito:** Big Panoche Creek (San Benito and Fresno County line), 5 mi S Bitterwater, 4 and 14 mi E Paicines, Panoche. **San Bernardino:** Big Morongo Creek (4 mi W Essex), 1 mi E East Highlands, Granite Mts., Kramer Hills, Mid Hills (9 mi SSE Cima), Mojave Desert, Pioneertown, Summit Valley. **San Diego:** Banner, Borrego Valley (including Culp Valley), 1 mi S Del Mar, Descanso–Alpine, Jacumba, Julian, McCain Valley, Mountain Springs Pass Oasis, Pena Spring, San Diego, Warner Springs. **San Luis Obispo:** 2.5 and 10 mi S Creston, La Panza (12 mi NE Pozo), Pozo, 4 mi SE Santa Margarita, 10 mi W Simmler. **Santa Barbara:** Santa Ynez Mts. **Trinity:** Hayfork. **Tulare:** Lemoncove. COLORADO: **Montezuma:** Mesa Verde National Park. NEVADA: **Clark:** Riverside, Valley of Fire State Park. **Lyon:** 13 mi NE Dayton. NEW MEXICO: **Dona Ana:** 5 mi E Las Cruces, Organ Mts. **Hidalgo:** Granite Pass.

MEXICO: **Baja California Norte:** Arroyo Santo Domingo, Catavиña (also 39 and 53 mi S), 0.9–4 mi S El Cóndor, Ensenada, 6 mi E Ojos Negros.

Tachysphex miwok sp. n.

(Figures 43, 44)

DERIVATION OF NAME.—Named after the Miwok Indians of California; noun in apposition.

DIAGNOSIS.—*Tachysphex miwok* is known only from California and adjacent areas of Nevada. Its distinctive features are: mesopleuron impunctate or with evanescent punctures, setae appressed, inclined on the hypoepimeral area, oriented posterad on scutum at middle and anterolaterad on the propodeal dorsum. In the female, the clypeal lip is not emarginate mesally nor incised laterally (Fig. 43a), and the femora and tibiae are black. Females of *tahoe* and *tipai* are similar, but their setae are erect on vertex and along the hypostomal carina, possibly with exceptions in *tahoe* in which the clypeal lip is sinuate (in *miwok* the setae are appressed on vertex and along the hypostomal carina, and the clypeal lip is arcuate). The clypeal lobe is slightly more prominent than in *antennatus* (in which most females also

Figure 42. Geographic distribution of *Tachysphex crenulatus* W. Fox.

have a laterally incised lip). Some undescribed species are also similar, but they differ by at least one of the following characters (characters in parentheses refer to *miwok*): (1) mesopleuron shallowly punctate, (2) surface of clypeal lip with several shallow concavities (clypeal lip evenly flat), (3) in some species foretarsomeres I and II with no less than seven and five rake spines, respectively, and six and five, or seven and four, in some individuals (tarsomeres I and II with three to six and two to four spines, respectively; Fig. 43b), (4) four or more apical spines of foretarsomere I with confluent or contiguous apical fossae (none, two, or three apical spines of tarsomere I with confluent or contiguous basal fossae, two in most specimens).

The male of *miwok* has appressed vertex setae and a relatively broad clypeal lobe (Fig. 43c): distance between lip corners equals 1.2–1.4× clypeal length. *Tachysphex antennatus, krombeini,* and *crassiformis* are similar. In *miwok,* however, the axilla is the usual shape (expanded in *crassiformis*), the outer apical spine of foretarsomere II is as long as foretarsomere III or longer (shorter in *antennatus* and *crassiformis*), the propodeum is not marginate or barely marginate between dorsum and hindface (marginate in the other three), and the gaster is all or partly red (all black in *krombeini,* some *antennatus,* and some *crassiformis*). The well-defined clypeal bevel is an additional recognition feature of *miwok.*

In both sexes, the clypeal, frontal, and mesopleural pilosity is finer and less dense than in *antennatus, crassiformis,* and *krombeini,* but the difference is difficult to describe or to quantify.

Description.—Punctures subcontiguous on frons, vertex, scutum, and mesothoracic venter. Mesopleuron dull, microsculptured, its punctures ill defined, shallow, subcontiguous. Propodeal dorsum and side microareolate, or (some specimens) side with ill-defined ridges, or (some females) side with conspicuous ridges (Lobos Creek, Lone Pine area, Quatal Canyon); hindface microridged or ridged. Sternum I without apical depression. Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit (except from certain angles). Setae appressed on vertex, beneath mesopleural scrobe, and on midfemoral venter; suberect on hypoepimeral area; oriented posterad on scutum at middle and anterolaterad on propodeal dorsum (except oriented posterad basally).

Head and thorax black, gaster red or largely black (see Variation below). Legs black, tarsal apex reddish. Terga I–III or (some males) I–IV silvery fasciate apically (fasciae inconspicuous in many specimens). Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 43a): bevel about as long as basomedian area; lip evenly arcuate, not emarginate mesally or incised laterally; free margin shallower between lip and orbit than in *antennatus* or *tarsatus.* Dorsal length of flagellomere I 1.8–2.0× apical width. Vertex width 1.0–1.5× length. Discal micropunctures of tergum II varying from one or two to several diameters apart. Tergum V with a few, sparse punctures, apical depression impunctate. Mid- and hindtrochanteral venter with minute, dense punctures, or partly impunctate. Length 5.0–7.5 mm.

♂.—Inner mandibular margin with tooth (Fig. 43c). Clypeus (Fig. 43c): bevel as long as basomedian area or shorter; lip truncate or arcuate, its corners obtuse, closer to orbits than to each other, separated by a distance that equals 1.2–1.4 of clypeal length. Dorsal length of flagellomere I 1.25–1.4× apical width. Vertex width 1.1–1.4× length. Sternal punctures minute, about as large as those on mesothoracic venter. Forefemoral notch glabrous. Forebasitarsus with none to two preapical rake spines;

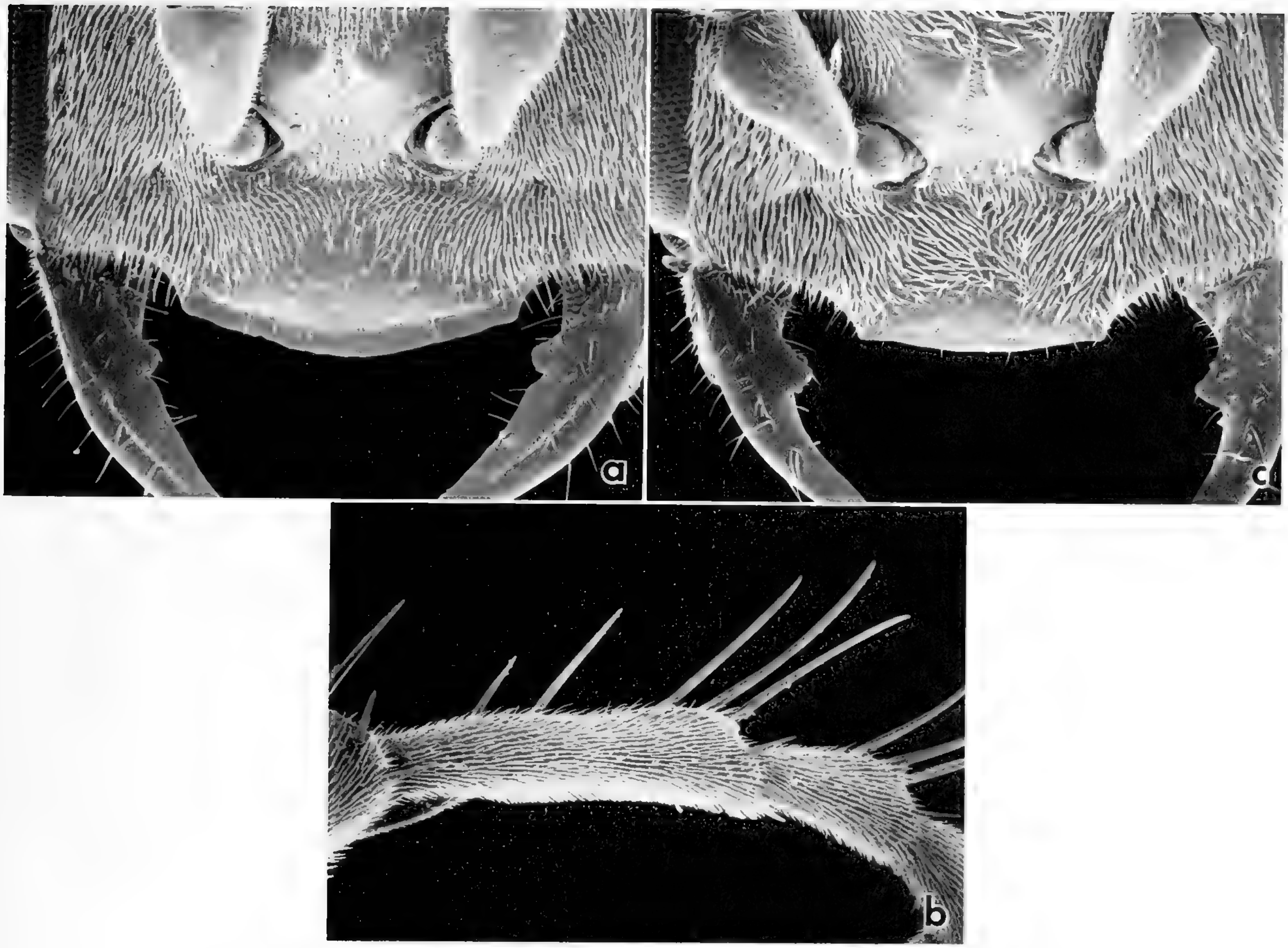

FIGURE 43. *Tachysphex miwok* sp. n.: a—female clypeus; b—basal articles of female foretarsus; c—male clypeus.

outer apical spine of foretarsomere II as long as foretarsomere III or longer. Length 5–6 mm.

VARIATION.—Vertex width : length ratio is about 1.2–1.5 (females) and 1.3–1.4 (males) in specimens from Monterey, San Francisco, and Marin counties, and also in the males from Canebrake Creek, California. This ratio is about 1.0 and 1.1, respectively, in remaining specimens studied.

Gaster red in most specimens, but in individuals from Monterey, San Francisco, and Marin counties, California, the gastral segment IV and the following ones are black (also segments I and III largely black in some specimens).

LIFE HISTORY.—A female from San Francisco (Laguna Puerca), California, is pinned with its prey: a 4.5-mm long nymph of an acridid, *Conozoa occidentalis* (Bruner), determined by D. C. F. Rentz.

GEOGRAPHIC DISTRIBUTION (Fig. 44).—California: Coastal Ranges between San Francisco and Los Angeles areas, and central and southern Sierra Nevada; also adjacent areas of Nevada and montane areas of Baja California Norte.

COLLECTING PERIOD.—3 March to 7 July.

MATERIAL EXAMINED.—Holotype: ♂, California: San Francisco Co.: San Francisco: Presidio Park, 30 May 1982, WJP (CAS, Type #14155).

Paratypes (61♀, 56♂; specimens for which institution is not indicated are in CIS): UNITED STATES: CALIFORNIA: **Fresno:** Jacalitos Canyon, RMB (1♂, UCD), DSH (1♀, UCD). **Inyo:** 7 mi SW Lone Pine, P. A. Opler (1♀), Tuttle Creek, 2 mi SW Lone Pine, P. A. Opler (1♀). **Kern:** Canebrake Creek, 3 mi W Walker Pass, JAP (1♂), C. A. Toschi (1♂); Walker Pass, C. A. Toschi (2♀, 2♂), W. D. Veirs (1♀) **Los Angeles:** Llano, J. C. Hall (1♀, UCD); Pearblossom, R. R. Snelling (2♂, CAS, LACM); 2 mi S Pearblossom, R. R. Snelling and E. Williams (1♀, LACM). **Marin:** Point Reyes, D. D. Linsdale (1♀, UCD), C. D. MacNeill (1♀, CAS), JAP (1♀); Point Reyes National Seashore, W. J. Turner (1♀, 1♂, WSU). **Mono:** 5 mi NW Paradise Camp, ASM (1♀, UCD), FDP (2♀, CAS; 1♀, UCD). **Monterey:** Asilomar, D. J Burdick (2♀, 3♂); Marina, MEI (3♂, UCR); Monterey, MSW (2♀, 2♂); Pacific Grove, MSW (2♀, 2♂, CAS: 2♀, 2♂, UCD); 1 mi S Soledad, JWMS (1♀). **Riverside:** Hemet Lake, MEI (1♂, UCR); Keen Campground, EIS (1♀, UCD); Whitewater Canyon, J. C. Hall (1♂, UCR). **San Benito:** Pinnacles National Monument, JWMS (1♀, UCD). **San Bernardino:** Apple Valley, N. McFarlane (1♀, LACM); 2 mi NE Baldwin Lake (San Bernardino Mts.), EIS (5♀); 4 mi S Barnwell, New York Mts., JAP (1♀); 9 mi SE Hesperia, E. Fisher (2♀, CAS, CSDA); Sheep Creek Canyon, A. L Melander (1♀, UCD); 5 mi S Victorville, PDH (2♂). **San Diego:** 5 mi SE Warner Springs, P. M. Estes (1♀, UCR). **San Francisco:** Fort Funston, G. I. Stage and R R. Snelling (1♂); Laguna Puerca, HKC (1♂), JAP (3♀, 7♂), J. R. Powers (1♂), R. R Snelling (1♀, UCD); Lobos Creek, PHA (1♂, CAS), HKC (2♀, 3♂), J. F. Lawrence (1♂), JAP (1♀, 4♂), D. C. F. Rentz, V. F. Lee, M. S. Carter, C. L. Mullinex (1♀, 2♂, CAS); Lone Mountain, FXW (1♀, UCD); Marine Hospital, JAP (1♀); San Francisco, E. P. Van Duzee (1♀, 1♂, UCD), FXW (1♂, CAS), San Francisco, sand dunes, C L. Fox (2♀, 1♂, UCD). **San Luis Obispo:** Dune Lake, 3 mi S Oceano, J. Doyen and JAP (1♀); Oso Flaco Lake, 5 mi S Oceano, JAP (4♂). **Ventura:** Hungry Valley (5 mi S Gorman), G. I. Stage (1♀); Lockwood Canyon near Stauffer P. O., G. I

FIGURE 44. Geographic distribution of *Tachysphex miwok* sp. n

Stage (1♀, 1♂), Lockwood Creek near Stauffer Post Office, JAP (3♂), G. I. Stage (1♂). Quatal Canyon (NW part of county), JAP (1♀), J. R. Powers (1♀). NEVADA Washoe: 1 mi S Mustang, FDP (1♀, UCD)

MEXICO. **Baja California Norte:** Las Encinas (Sierra San Pedro Mártir), JWB and DKF (1♀, SDNH); 6 mi N Laguna Hanson (Sierra de Juárez), collector not indicated (1♂, SDNH)

Tachysphex krombeini Kurczewski

(Figures 45, 47)

Tachysphex sp. No. 3: Krombein and Evans 1954:233, 1955:231.
Tachysphex krombeini Kurczewski, 1971:111, ♂, ♀. Holotype: ♂, Florida: Desoto Co.: Arcadia (USNM).—Bohart and Menke 1976:274; Krombein 1979:1628.

DIAGNOSIS.—*Tachysphex krombeini* is an all black species with ill-defined mesopleural punctures which occurs in the southeastern United States (North Carolina to Florida and Alabama). Like most *antennatus* and most *crassiformis*, the propodeal dorsum of *krombeini* is relatively flat, not sloping posteriorly toward the transverse carina that separates it from the hindface. It differs from these two species in having a slightly more prominent clypeal lobe (compare Fig. 45a and 46a); in the female the pygidial plate is markedly alutaceous (Fig. 45b), at least basally (not or weakly alutaceous in the other two); in the male, the forebasitarsus has three or four preapical rake spines (no preapical spines in the other two or two to four such spines present in occasional *antennatus* from California). Unlike most *crassiformis*, the axilla is simple in *krombeini*.

Tachysphex krombeini also resembles *tarsatus* and *williamsi* in having mesopleural setae appressed or weakly inclined, but their clypeus is slightly different (compare Fig. 45a and 34a). Unlike *krombeini*, the propodeal dorsum of these species slopes posterad toward the transverse carina that separates it from the hindface (though slightly so in some specimens), and the males have distinctive sternal setae. Furthermore, *williamsi* is a western species, and southeastern populations of *tarsatus* have a red gaster.

DESCRIPTION.—Frons dull, its punctures shallow, ill defined, subcontiguous. Vertex and scutum punctate, punctures less than one diameter apart. Mesopleuron dull, its punctures fine, ill defined, subcontiguous. Propodeal dorsum evenly microareolate; side dull, microridged, or (mostly in males) evenly microareolate; hindface ridged, margined above by sharp, mesally interrupted carina. Sternum I with apical depression. Discal micropunctures of tergum II two to three diameters apart. Hindcoxa carinate.

Vestiture almost completely obscuring integument between antennal socket and orbit, partly hiding mesopleural sculpture. Setae appressed on vertex, scutum, and femora, appressed or weakly inclined on mesopleuron.

Body black, tarsal apex dark brown; apical depression of terga II and III testaceous in many specimens. Terga I–IV silvery fasciate apically. Frontal vestiture silvery. Wings faintly infumate.

♀.—Clypeus (Fig. 45a): bevel shorter than basomedian area; lip arcuate, not incised laterally to almost straight, laterally incised. Dorsal length of flagellomere I 1.7–1.9× apical width. Vertex width 1.1–1.2× length. Tergum V densely punctate, except apical depression largely impunctate. Pygidial plate sparsely punctate, in most specimens coarsely microsculptured (Fig. 45b), at least basally. Trochanters and femora evenly micropunctured. Length 5.0–6.5 mm.

♂.—Mandibular inner margin with tooth (Fig. 45c). Clypeus (Fig. 45c): bevel shorter than basomedian area; lip evenly arcuate, its corners obtuse, closer to orbit than to each other,

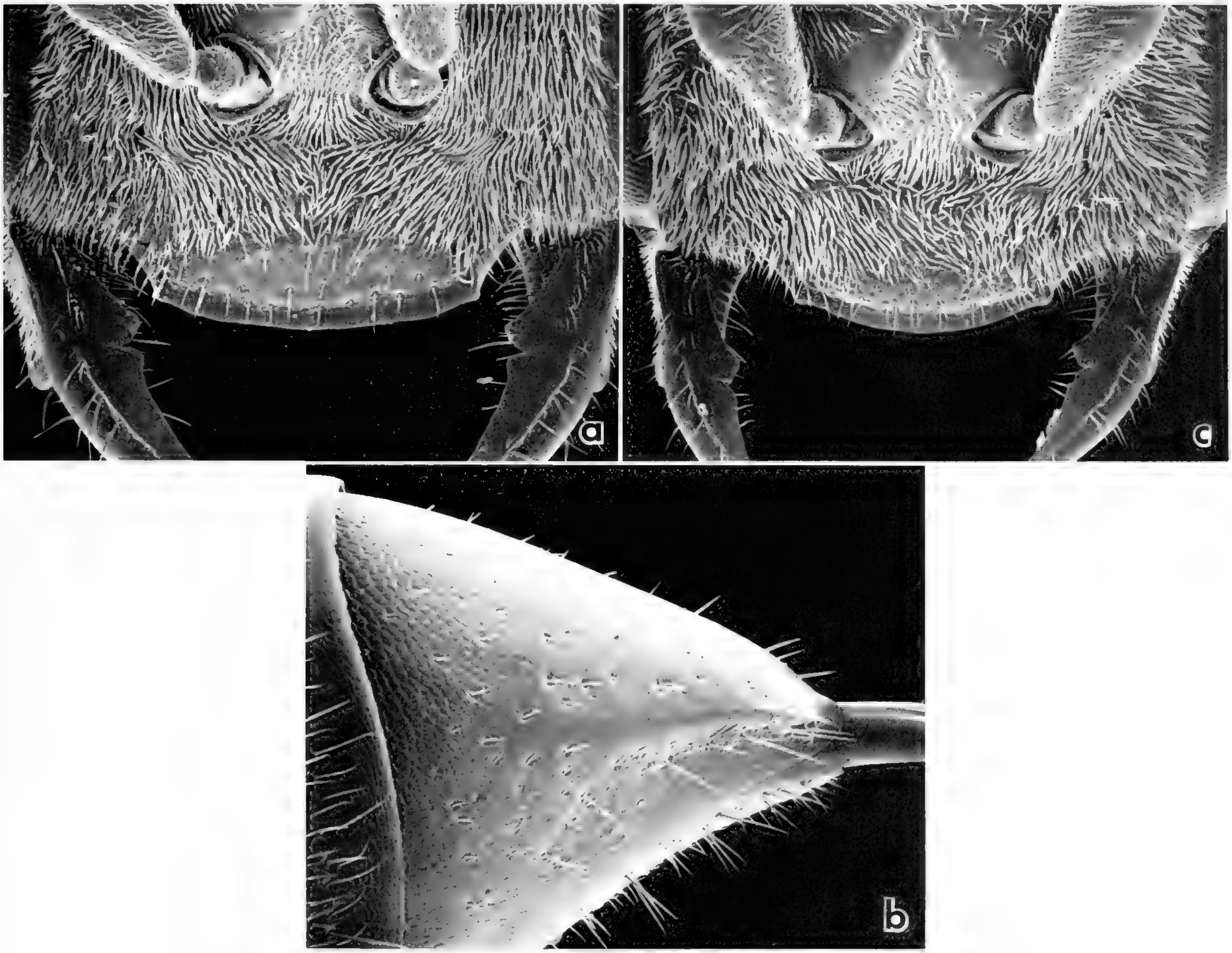

FIGURE 45. *Tachysphex krombeini* Kurczewski: a—female clypeus; b—pygidial plate of female; c—male clypeus.

separated by a distance that equals 1.3–1.5 of clypeal length. Dorsal length of flagellomere I 1.1–1.4× apical width. Vertex width 1.8–2.0× length. Sterna punctate throughout. Forefemoral notch glabrous. Forebasitarsus with three or (some individuals) four preapical rake spines that are slightly shorter to slightly longer than basitarsal width; outer apical spine of foretarsomere II slightly shorter than tarsomere III. Length 4–5 mm.

LIFE HISTORY.—*Tachysphex krombeini* has been studied by Kurczewski (1971). The species nests in sparsely vegetated sandy areas and appears from the end of March to at least the end of June; consequently, there must be at least two generations per year. A nest observed at Arcadia, Florida, was permanently open during the provisioning period. The burrow, 3 mm in diameter, entered the sand at an angle of about 37° to the horizon and terminated in a small, oval cell 2.8 cm beneath the surface. The sand removed from the burrow formed a tumulus. Prey were brought to the nest in flight. The wasp held the prey under her body with her legs, grasping its antennae with her mandibles. She plunged into the entrance, quickly releasing the prey just inside. She reappeared headfirst and, grasping the prey by its antennae with her mandibles, backed into the nest. Each prey was deposited venter up, and this fact suggests that they were carried to the nest in this position. The cell contained six nymphs of *Melanoplus* sp. (Acrididae) and one nymph of *Odontoxiphidium apterum* Morse (Tettigoniidae). All were arranged head inward; five acridids (including the egg-bearer) venter up, two remaining dorsum up. The wasp's egg was attached by the cephalic end to the soft corium surrounding the base of the largest acridid's left forecoxa and laid transversely behind the forelegs. After completing provisioning, the female raked sand backward with the forelegs bent mesad, then she backed into the burrow while raking and packed the sand into the tunnel with the bent end of her gaster. While hammering with her pygidium, she held her antennal tips against the wall of the burrow.

GEOGRAPHIC DISTRIBUTION (Fig. 47).—North Carolina to Alabama and Florida.

MATERIAL EXAMINED.—25♀, 12♂, including 9♀, 8♂ paratypes (CAS, CU, FSCA KVK, MCZ, NYSU, UGA, USNM, WJP)

Records.—UNITED STATES: ALABAMA: **Baldwin:** Gulf Shores. FLORIDA: **Alachua:** Gainesville, Monteoca (11 mi NW Gainesville). **Desoto:** Arcadia. **Gadsden:** Quincy. **Glades:** Palmdale. **Hernando:** 4 mi NE Lacoochee. **Highlands:** Lake Placid (Archbold Biological Station). **Lee:** Olga. **Liberty:** Torreya State Park. **Okaloosa:** 1.7 mi N Holt. **Orange:** Orlando. GEORGIA: **Lanier:** Lakeland. NORTH CAROLINA: **Cumberland:** Fort Bragg

Tachysphex antennatus W. Fox

(Figures 46, 47)

Tachysphex antennatus W. Fox, 1894*a*:516, ♀. ! Holotype: ♀, Texas: no specific locality (ANSP).—Dalla Torre 1897:678; Ashmead 1899:250; Rohwer 1911: 580 (in key). Cresson 1928:43; G. Bohart 1951:950, Bohart and Menke 1976: 272; Krombein 1979:1628; Elliott and Kurczewski 1985:293.

Tachysphex sculptiloides Williams, 1914:166, ♀. ! Holotype: ♀, Kansas: Barton Co.: no specific locality (KU). Synonymized by Pulawski *in* Krombein 1979: 1628.—G. Bohart 1951:952; LaBerge 1956:528, Arnaud 1970:33; Bohart and Menke 1976:276

Tachysphex nigrocaudatus Williams, 1914:167, ♀, ♂. ! Holotype: ♀, Kansas: Rush Co., no specific locality (KU). Synonymized by Pulawski *in* Krombein 1979: 1628.—Mickel 1918:424; Brimley 1938:443; G. Bohart 1951:951; LaBerge 1956: 527, Arnaud 1970:32, Bohart and Menke 1976:275

Diagnosis.—*Tachysphex antennatus* has an unusually broad clypeal lobe (Fig. 46a, d): the distance between its corners equals 1.8–2.5 × the clypeal length in the female and 1.5–1.6 × in most males. Clypeal proportions are identical or similar in several other species, but in *antennatus* the vertex setae are appressed (erect in *pinal* and *toltec*) and the axilla slopes gradually (axilla steplike or expanded in *crassiformis* and *paiute*, see these species for further differences). In most females, the clypeal lip is incised laterally and the legs are black (lip not incised and hindfemur and hindtibia all or partly red in *occidentalis*), but in some specimens the lip is entire, and in some others the hindlegs are all or largely red (these two conditions are rare and presumably do not occur together in the same specimen). *Tachysphex antennatus* is also similar to *cubanus*, *miwok*, and *krombeini* and can be separated by the characters given under these species (pages 77, 67 and 70).

The clypeal lobe is narrow in some males of *antennatus* (distance between lobe corners about 1.2 × clypeal length). Such individuals can be recognized by a nearly straight clypeal lip combined with appressed mesopleural vestiture.

Description.—Punctures less than one diameter apart on frons, vertex, and scutum (more than that in some females) and on mesothoracic venter. Mesopleuron microsculptured, with minute punctures (Fig. 46b) that are inconspicuous in many specimens. Propodeal dorsum evenly microareolate, rugose in some specimens, not sloping or barely sloping toward transverse carina that separates it from hindface; carina well defined except absent laterally in smallest specimens; side and hindface ridged (Fig. 46c), but ridges largely evanescent in some specimens. Apical depression of sternum I absent or ill defined. Discal micropunctures of tergum II about two to three diameters apart. Hindcoxa carinate except in smallest males.

Integument visible between antennal socket and orbit from certain angles in female, from many angles in male. Setae appressed, shorter than 1.0 MOD on vertex; oriented evenly posterad to transversely on midscutum; appressed to inclined on mesopleuron; basal setae of propodeal dorsum oriented posterad and laterad; nearly appressed on scutum and midfemoral venter.

Head, thorax, and legs black, tarsal apex brown, hindtibia red in some females from Animas area, New Mexico. Wings weakly infumate. Frontal vestiture silvery or with golden tinge.

♀.—Clypeus (Fig. 46a): lobe broad (distance between lip corners 1.8–2.5 × clypeal length); bevel longer than basomedian area, equal in some specimens; lip weakly arcuate or weakly sinuate, not emarginate mesally, incised laterally or (some specimens) entire. Dorsal length of flagellomere I 1.6–1.9 × apical width. Vertex width 1.2–1.4 × length. Tergum V sparsely punctate mesally, its apical depression impunctate. Pygidial plate shiny, sparsely punctate. Trochanters and forefemoral venter finely, closely punctate. Length 5.5–8.0 mm.

Gaster red to black, terga I–III or I–IV silvery fasciate apically.

♂.—Mandibular inner margin with tooth (Fig. 46d). Clypeus (Fig. 46d): lobe almost flat, of varying width (see Individual Variation below), with weakly sinuate free margin; its corners obtuse but well defined; bevel shorter than basomedian area. Dorsal length of flagellomere I 1.0–1.4 × apical width. Vertex width 1.3–2.1 × length. Sterna evenly, densely punctate throughout, punctures finer than those on mesothoracic venter. Forefemoral notch finely pruinose. Forebasitarsus with none to four preapical rake spines that are no longer than basitarsal width (see Individual Variation below). Length 4.5–6.0 mm.

Gaster black or segments I–III red, terga I–IV or I–V silvery fasciate apically.

Individual Variation.—In most females, terga I and II or I–III are red, and the remainder is black. The gaster is all red in many western specimens, but it is all black in many females from Texas, California, Nevada, a female from Teotihuacán, Mexico, and a female from Osoyoos, British Columbia.

In most males, the foretarsal rake is absent (only the apical spine is present), and the outer apical spine of foretarsomere II is shorter than tarsomere III. However, some black specimens from Carnelian Bay, California, have two apical spines on foretarsomeres I and II. In a few specimens from the same locality, there are three or four rake spines on the forebasitarsus, and the outer apical spine of foretarsomere II is as long as tarsomere III. The gaster is black in most males, but segments I–III are red in many individuals from California.

In most males, the clypeal lip is weakly arcuate, and its corners are closer to the orbit than to each other; they are separated by a distance equal to 1.5–1.6 of the clypeal length. The clypeus is exceptionally narrow in three males from Sycamore Canyon, Arizona: the lip is straight or weakly emarginate, and its corners are closer to each other than to the orbits (as 0.8:1); they are separated by a distance equal to 1.2–1.3 of the clypeal length.

Geographic Variation.—Eastern and western populations of *antennatus* differ in thoracic sculpture and pilosity, as discussed below. The differences, some of them easy to observe but difficult to describe or to quantify, are probably correlated with the humidity of the respective habitats. In the eastern specimens, mesopleural micropunctures are smaller, less conspicuous; mesopleural setae are somewhat less dense and more inclined; ridges of the propodeal side are slightly finer and denser; and setae of the propodeal dorsum are oriented anterad along the midline; in the female, scutal punctures are close to each other, almost contiguous. This form is distributed from the East Coast throughout Mexico, southeastern Arizona, and Colorado. In the western specimens, mesopleural micropunctures are larger, more conspicuous; mesopleural setae are slightly denser and less inclined; ridges of the propodeal side are slightly larger and less dense; and setae of the propodeal dorsum are oriented anterolaterad, parted along midline; in the female, scutal punctures

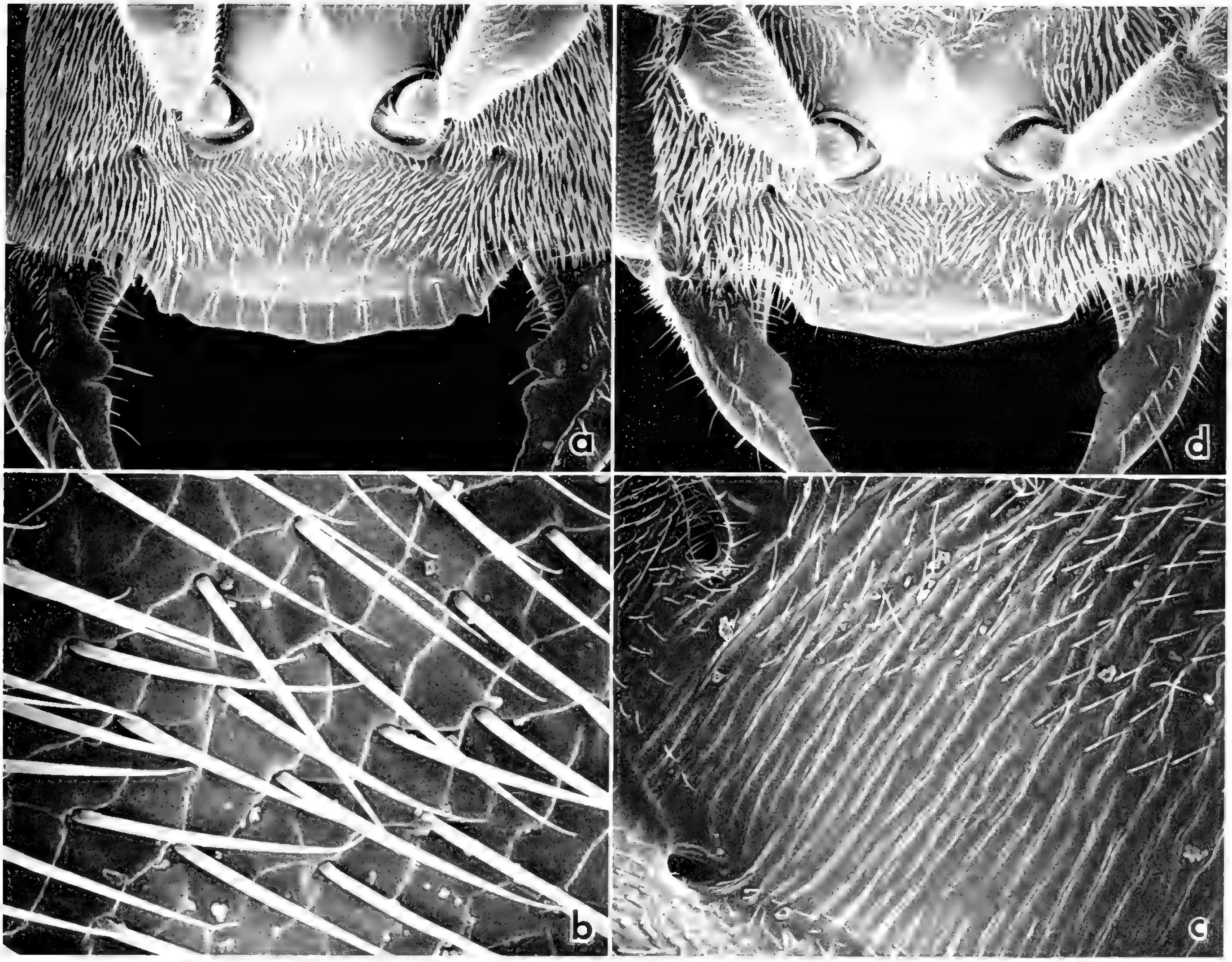

FIGURE 46. *Tachysphex antennatus* W. Fox: a—female clypeus; b—sculpture of female mesopleuron; c—sculpture of propodeal side of female; d—male clypeus

are two to four diameters apart on each side of the median zone. The western form occurs between the West Coast and the Rocky Mountains.

LIFE HISTORY.—Specimens from Animas area, New Mexico, were collected on flowers of *Baccharis glutinosa* Pers. Elliott and Kurczewski (1985:293) noted two females carrying nymphal acridids, *Melanoplus* sp. in short, low flights at Erie, Pennsylvania.

GEOGRAPHIC DISTRIBUTION (Fig. 47).—Southwestern Canada, United States, Mexico.

MATERIAL EXAMINED.—832♀, 684♂.

RECORDS.—CANADA: **British Columbia:** Osoyoos (Richter Pass).

UNITED STATES: ARIZONA: **Cochise. Gila:** San Carlos. **Graham:** Roper Lake State Park. **Maricopa:** road 74 5 mi W road 17. **Mohave:** Bullhead City, Mohave Valley. **Pima:** Madera Canyon, Sabino Canyon, Tucson (also 10 mi NE). **Santa Cruz.** CALIFORNIA: **Alameda:** Sycamore Grove State Park. **Alpine:** Hope Valley, Winnemucca Lake. **Butte:** 20 mi N Yuba City. **Colusa:** 21 mi SW Williams. **Contra Costa:** Antioch, Moraga, Mt. Diablo. **El Dorado. Fresno:** Coalinga (also 8 mi NW) **Glenn:** Plaskett Meadows. **Inyo. Kern. Lake:** Borax Lake, N Fork Cache Creek at Highway 20. **Lassen:** Hallelujah Junction, Norvell, Summit Camp (E Lassen Peak). **Los Angeles. Marin:** Point Reyes. **Modoc. Mono. Monterey:** Arroyo Seco, Monterey, Soledad. **Napa:** Samuel Spring (now bottom of Lake Berryessa) **Nevada. Orange:** Laguna Canyon, Peters Canyon, Potrero Canyon. **Placer. Plumas:** Buck's Lake, 6 mi E Chester, Quincy. **Riverside. Sacramento:** Sacramento **San Benito:** Pinnacles National Monument. **San Bernardino. San Diego. San Francisco:** San Francisco (Laguna Puerca, Lobos Creek, Marine Hospital, Presidio Park). **San Joaquin:** Stockton **San Luis Obispo. San Mateo:** San Bruno. **Santa Barbara:** 4 mi E Los Prietos. **Santa Cruz:** Felton, Laurel **Shasta:** Hat Creek Post Office, Hat Lake (NE Lassen Peak), Moose Camp **Sierra. Siskiyou. Trinity:** Hayfork **Tulare:** Fairview, Lemoncove **Tuolumne. Ventura:** 5 mi S Gorman, Lockweed Creek near Stauffer Post Office, 1 mi W Santa Susana **Yolo. Yuba:** 18 mi S Marysville COLORADO: **Bent:** Hasty **Boulder:** Boulder **Denver:** Denver **Fremont:** Canon City **Gunnison:** Lead King Basin. **Jefferson:** Clear Creek, Morrison. **Larimer:** Fort Collins (Flatiron Site, e) DISTRICT OF COLUMBIA. Washington. FLORIDA: **Alachua:** Gainesville GEORGIA **Clarke:** Athens, Whitehall Forest IDAHO **Bear Lake:** Paris **Cassia:** 7 and 8 mi SW Malta. **Fremont:** Saint Anthony Sand Dunes **Lincoln:** Dietrich Butte, Owynza, 7 mi W Shoshone ILLINOIS **Champaign:** Trealese Woods **Williamson:** Crab Orchard Lake IOWA **Woodbury:** Sioux City KANSAS **Barton:** — **Douglas:** Baldwin **Ellis, Ness:** — **Gray:** Cimarron **Pottawatomie:** Onaga **Riley:** Manhattan **Rush:** — **Stafford:** Salt Marsh LOUISIANA: **St. Landry:** Opelousas. MARYLAND **Montgomery:** Colesville, Penny Field Locks MICHIGAN: **Cheboygan, Livingstone:** — **Washtenaw:** Ann Arbor (Matthaei Botanical Garden), Half Moon Bay Pinckney Recreation Area MISSOURI **Boone:** Columbia **Jackson:** Atherton **Vernon:** Nevada MONTANA **Rosebud:** Ashland NEBRASKA. **Adams:** Hastings. **Dawes:** Chadron **Hall:** 6 mi W Cairo NEVADA. **Churchill:** Carson Sink **Douglas:** Minden, Spooners Lake (N Junction Highway 28) **Elko:** 7 mi NE Carlin. **Mineral:** 4 5 mi S Schurz **Nye:**

FIGURE 47 Geographic distribution of *Tachysphex antennatus* W. Fox and *krombeini* Kurczewski.

4 mi S Warm Springs. **Washoe.** NEW HAMPSHIRE: **Rockingham:** Hampton. NEW JERSEY: **Bergen:** Mahwah. **Mercer:** Princeton. **Morris:** Long Valley. NEW MEXICO: **Colfax:** Raton. **De Baca:** Sumner Lake State Park. **Dona Ana:** 5 mi E Las Cruces, Leesburg Dam State Park. **Hidalgo:** 15 mi S Animas. **Otero:** Alamogordo. **Sierra:** Percha Dam State Park. NEW YORK: **Albany:** Rensselaerville. **Rensselaer:** Brainard. **Suffolk:** Huntington. **Tompkins:** Ithaca. **Westchester:** Lewisboro. NORTH CAROLINA: **Wake:** Raleigh. OHIO: **Summit:** Barberton. OKLAHOMA: **Cimarron:** Black Mesa State Park. OREGON: **Crook:** Powell Butte. **Deschutes:** Smith Rock State Park. **Malheur:** 3 mi S Vale. **Morrow:** Boardman. PENNSYLVANIA: **Erie:** Erie. **York:** 5 mi NW Davidsburg. **Westmoreland:** Jeanette. SOUTH DAKOTA: **Bon Homme:** Springfield. TEXAS: **Anderson:** Salmon. **Bastrop:** 6 mi E Bastrop. **Bexar:** Fort Sam Houston. **Brazos:** College Station. **Brewster:** 9 mi S Alpine. **Hudspeth:** McNary. **Jeff Davis:** near Point of Rocks (10 mi W Fort Davis). **Kimble:** Junction. **Kleberg:** Kingsville (also 20 mi SE). **Lee:** Fedor. **Midland:** Midland. **San Patrizio:** Aransas River 10 mi NE Sinton. **Somervell:** Dinosaur Valley State Park. **Uvalde:** 30 mi N Uvalde. UTAH: **Cache. Garfield:** Boulder. **Kane:** Kanab. **Millard:** Delta. **Uintah:** SW Bonanza, Green River (5 mi NE Jensen), road 44. **Washington:** 1 mi W Leeds. **Weber:** Willard Peak. VIRGINIA: **Arlington:** Arlington. **Fairfax:** Alexandria, Clifton, Dunn Loring near Vienna. WEST VIRGINIA: **Hardy:** Lost River State Park. WYOMING: **Sweetwater:** Green River.

MEXICO: **Baja California Norte:** Cataviña (also 39 and 53 mi S), 4 mi S El Cóndor, Ensenada, Laguna Hanson (41 mi S La Rumorosa), Progreso (Sierra Juárez), 1 mi E Santa Inés, 8 mi E Tecate, 12.3 mi S Valle de las Palmas. **Baja California Sur:** La Purisima (6.8 mi S San Juanico), 16 mi S Rosarito. **Chiapas:** San Cristóbal de las Casas (also 21 mi E). **Chihuahua:** 15 mi E Cuauhtémoc, Santa Clara Canyon 5 mi W Parrita. **Durango:** 7, 10, and 25 mi W Durango. **Jalisco:** El Tigre, Estanzuela (40 km W Ameca), Guadalajara (also 15 and 16 mi NE), Ixtlahucán del Río, 6 mi S Ojuelos, 8 mi NW Tequila, Villa Guadalupe. **México:** Teotihuacán Pyramids. **Morelos:** 4 mi E Cuernavaca. **Oaxaca:** Oaxaca. **Sonora:** Alamos, 15–25 km NW Yecora. **Tamaulipas:** 80 km S Ciudad Victoria, 15 mi N Llera. **Veracruz:** Fortín de las Flores. **Zacatecas:** 15 km E Sombrerete.

Tachysphex crassiformis Viereck

(Figures 48, 49)

Tachysphex crassiformis Viereck, 1906:210, ♀. ! Holotype: ♀, Kansas: Hamilton Co.: no specific locality (KU).—Williams 1914:168; G. Bohart 1951:950; LaBerge 1956:527; Bohart and Menke 1976:273; Krombein 1979:1627.

Tachysphex wheeleri Rohwer, 1911:579, ♀. ! Holotype: ♀, Texas: Lee Co.: no specific locality (USNM). Synonymized by Pulawski *in* Krombein 1979:1628.—G. Bohart 1951:953; Krombein 1967:394; Bohart and Menke 1976:277.

Tachysphex plenoculiformis Williams, 1914:167, ♀. ! Holotype: ♀, Kansas: Ness Co.: no specific locality (KU). Synonymized by Pulawski *in* Krombein 1979:1628.—Williams 1914:201; G. Bohart 1951:952; LaBerge 1956:527; Arnaud 1970:32; Bohart and Menke 1976:275.

Tachysphex n. sp.: Krombein 1949:267, 1953*a*:330, 1953*b*:132.

Tachysphex sp. No. 4: Krombein and Evans 1955:231

Tachysphex boharti Krombein, 1963*a*:177, ♀, ♂. ! Holotype: ♀, North Carolina: Dare Co.: Kill Devil Hills (USNM). Synonymized by Pulawski *in* Krombein 1979:1628.—Krombein 1967:392; Wray 1967:123; Kurczewski 1971:114 (in key); Bohart and Menke 1976:272.

Tachysphex gibbus Pulawski, 1974*a*:20, ♀, ♂. ! Holotype: ♀, El Salvador: Quezaltepeque (UCD). Synonymized by Pulawski *in* Krombein 1979:1628.—Bohart and Menke 1976:274.

Diagnosis.—Most *crassiformis* have a prominent scutal hindcorner and an expanded or steplike axilla (Fig. 48b, d, e), two characters shared only with *paiute*. The midscutal gibbosity (Fig. 48c) present in some individuals is not found in any other *Tachysphex*. Unlike *paiute*, the hypostomal carina of *crassiformis* is low (the usual size), the adjacent setae are shorter than MOD, and in the male the free margin of the clypeal lobe is arcuate. The axilla is slightly expanded or not expanded in some females, and such specimens resemble *antennatus* because of the unusually broad clypeal lobe (lobe width 1.7–2.0 clypeal length), a similar sculpture of the mesopleuron, and appressed vertex setae. Details of body vestiture help in identification: in *crassiformis*, the mesopleural setae partly conceal the mesopleural integument, and the propodeal setae are oriented anterad along the midline; in *antennatus*, the mesopleural integument is easily visible, and in the western populations the setae of the propodeal dorsum are parted along the midline, diverging anterad. *Tachysphex krombeini* is also similar, but the clypeal lobe is slightly more prominent (compare Fig. 48a and 45a), and the gaster is black (all or partly red in *crassiformis*).

Description.—Frons microsculptured, its punctures subcontiguous to more than one diameter apart, inconspicuous in some individuals. Vertex and scutal punctures less than one diameter apart or scutal punctures several diameters apart. Reflexed marginal flange of scutum prominently expanded at posterior corner (Fig. 48b, d, e). Axilla (except some females) expanded laterally into a lobe which may be large (overhanging lateral fossa) or small, steplike; its lateral outline markedly arcuate in dorsal view (Fig. 48b, d, e). Mesopleuron finely, evenly punctate, punctures almost contiguous. Metapleural flange broadened in some specimens. Propodeal dorsum evenly microareolate; side and hindface ridged, ridges evanescent in some specimens; hindface margined above by sharp, mesally interrupted carina (which may be absent laterally in smallest specimens). Apical depression of sternum I indistinct or absent. Discal micropunctures of tergum II evanescent, two to three diameters apart. Hindcoxa carinate.

Vestiture concealing sculpture between antennal socket and orbit, partly hiding mesopleural sculpture. Setae appressed on vertex, scutum, and femora, appressed or nearly so on mesopleuron; midscutal setae variably oriented (longitudinally to transversely); setae of propodeal dorsum oriented anterad, at least on mesal zone; only a few setae oriented anterad in a female (20 mi S Portal, Arizona, CAS) whose identification is unquestionable because of the markedly expanded axilla.

Terga I–IV or (some males) I–V silvery fasciate apically. Frontal vestiture silvery. Wings almost hyaline.

♀.—Clypeus (Fig. 48a): lobe broader than in most other species (distance between lip corners 1.7–2.0× clypeal length); bevel longer to shorter than basomedian area; lip weakly arcuate, incised laterally or entire (even in members of the same population). Dorsal length of flagellomere I 1.6–2.1× apical width. Vertex width slightly more to slightly less than length. Tergum V with a few scattered punctures, its apical depression impunctate. Pygidial plate alutaceous, sparsely punctate. Trochanters and forefemoral venter evenly micropunctate. Length 5.5–8.0 mm.

Head and thorax black, but propodeum and thoracic venter partly red in some specimens from Portal, Arizona; gaster all red (most specimens) to almost all black (some individuals). Legs black or hindlegs largely red, and all legs red in occasional females from Portal, Arizona; tarsal apex brown.

♂.—Mandibular inner margin with tooth (Fig. 48f). Clypeus (Fig. 48f): lobe almost flat, relatively broad (distance between lip corners 1.6–1.8× length); bevel shorter than basomedian area; lip arcuate, its corners obtuse to acute, not prominent, closer to orbit than to each other. Dorsal length of flagellomere I 1.0–1.5× apical width. Vertex width 1.8–2.2× length. Sterna usually densely punctate throughout, but sterna III–V sparsely punctate in some Arizona specimens. Forefemoral notch weakly pubescent. Foretarsus in most specimens without rake (see Variation for further details); outer apical spine of foretarsomere II much shorter than foretarsomere III. Length 4.0–5.5 mm.

Head, thorax, and legs black, hindtibia and tarsal apex sometimes brown. Gaster black or segments I–III red.

Variation.—Scutum weakly, evenly convex (most specimens

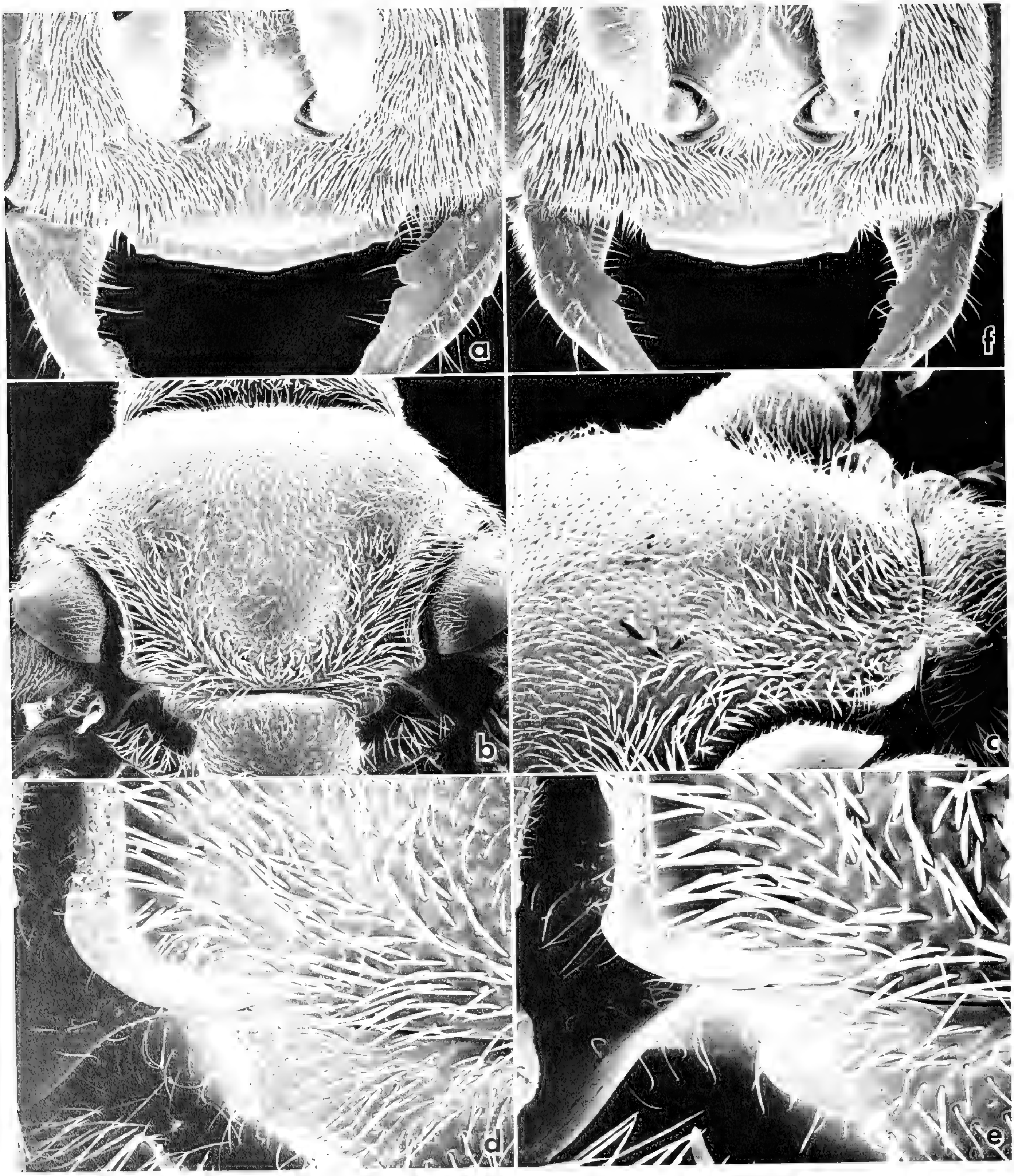

FIGURE 48. *Tachysphex crassiformis* Viereck. a—female clypeus, b—female scutum, dorsal view; c—same of a different specimen, oblique view; d—scutal hindcorner and axilla of female, weakly expanded, e—same, broadly expanded, f—male clypeus.

from United States) or with variably developed mesal gibbosity (which is high south of Mexico).

Scutal puncture in most specimens less than one diameter apart, but in some females (holotype of *crassiformis*, a specimen from Fort Collins, Colorado; one from White Rocks, Colorado; one from Continental, Arizona) most discal punctures are several diameters apart, and intermediates occur.

The foretarsal rake is usually absent in the male, but some individuals from Kill Devil Hills, North Carolina, and Death Valley Junction, California, have one or two preapical spines on the forebasitarsus. These spines may be as long as the basitarsal width.

Life History.—The nesting behavior of *crassiformis* was observed by Williams (1914) and Krombein (1963*a*). The species is apparently restricted to sparsely vegetated sandy areas. There are at least two generations a year. The nest has a single cell, and its entrance is left open during the provisioning period. The recorded prey are nymphal Acrididae: *Psinidia fenestralis* (Serville), *Scirtetica marmorata picta* (Scudder), and unidentified acridines (=tryxalines). Small nymphs are flown to the nest, but prey larger than the wasps are carried on the ground with occasional, short flights; they are held venter up under the body of the wasp which grasps them by their antennal bases. The number of prey per cell varies from one (Krombein) to six (Williams), according to their size. Arriving at the nest, the female flies directly to the burrow with the grasshopper (Williams, small prey) or deposits it at the entrance and then pulls it in (Krombein, large prey). The egg is attached transversely to the sternum behind the forecoxae or to the throat of the prey.

Geographic Distribution (Fig. 49).—United States from North Carolina, Wyoming, Idaho, and central California south to Florida, Texas, Venezuela, and Colombia, north to southern Alberta.

Material Examined.—695♀, 463♂ (including 22♀, 4♂ paratypes of *boharti*).

Records.—CANADA: **Alberta:** 12 km SW Orion, Writing-on-Stone Provincial Park.

UNITED STATES: ALABAMA: **Baldwin:** Gulf Shores. **Montgomery:** Montgomery. ARIZONA: **Cochise. Coconino:** Antelope Hills (25 mi N Flagstaff), Flagstaff. **Gila:** 7 mi N Payson, Strawberry. **Graham:** Dripping Springs (Whitlock Mts.), Roper Lake State Park (6 mi S Safford). **Maricopa:** Phoenix, 3 mi SW Wickenburg (also 5 mi SE). **Mohave:** 4 mi W Chloride, Wikieup. **Pima. Pinal:** Boyce Thompson Arboretum (3 mi W Superior), 3 mi W Oracle. **Santa Cruz:** Nogales, 6 and 12 mi SW Patagonia, Sycamore Canyon. **Yavapai:** 7 mi E Cottonwood, 8 mi NE Yarnell. ARKANSAS: **Conway:** —. CALIFORNIA: **Imperial:** Glamis (also 20 mi E), Palo Verde (also 3 mi S), Picacho Recreation Area (18 mi N Winterhaven). **Inyo. Kern:** Antelope Canyon near Tehachapi. **Los Angeles:** Long Beach. **Mono:** East Walker River (13 mi NE Bridgeport). **Orange:** Laguna Canyon, Newport Beach, Santa Ana Canyon. **Riverside:** 6 mi NE Blythe (also 18 mi W), Deep Canyon (4 mi S Palm Desert), Riverside. **San Bernardino. San Diego. SantaBarbara:** Los Prietos. **Tulare:** Goshen Junction. **Ventura:** Wagon Road No. 2 Campground (18 air mi WSW Gorman). COLORADO: **Bent:** Hasty. **Boulder:** White Rocks near Boulder. **Denver:** Denver. **Larimer:** Park Creek (20 mi N Fort Collins). **Montezuma:** 3 mi W Arriola. **Prowers:** Lamar. **Teller:** Florissant. **Weld:** Owl Creek (12 mi NE Nunn), Pawnee National Grassland (8 and 11 mi NE Nunn), 1 mi NE Roggen. FLORIDA: **Alachua:** Gainesville, Monteoca (11 mi NW Gainesville), San Felasco Hammock. **Citrus:** —. **De Soto:** Arcadia. **Gadsden:** Quincy. **Levy:** Cedar Key, Shell Mound. **Liberty:** Torreya State Park. **Nassau:** Fort Clinch State Park. **Putnam:** Welaka. **St. Lucie:** Fort Pierce. GEORGIA: **Liberty:** St. Catherine's Island. **McIntosh:** Sapelo Island. IDAHO: **Fremont:** 6 mi NW Saint Anthony. **Gooding:** 1 mi NE Gooding. **Owyhee:** Bruneau. KANSAS: **Ellis:** Hays. **Grant, Hamilton:** —. **Kearny:** Lakin. **Ness, Norton, Stanton:** —. MONTANA: —. NEBRASKA: **Buffalo:** 10 mi SE Ravenna. NEVADA: **Churchill:** Carson Sink, 3 mi W Hazen. **Clark:** 8 mi S Overton. **Douglas:** Teels Marsh sand dunes. **Lyon:** Fernley. **Storey:** 15 mi E Reno. NEW MEXICO: **Catron:** Glenwood, Pie Town. **Colfax:** —. **De Baca:** Sumner Lake State Park. **Dona Ana:** Las Cruces. **Eddy:** Carlsbad. **Hidalgo. Los Alamos:** Los Alamos. **Otero:** Alamogordo. **San Juan:** 43 mi S Shiprock. **Sierra:** Percha Dam State Park. **Socorro:** La Joya (20 mi N Socorro). NORTH CAROLINA: **Dare:** Kill Devil Hills, Salvo. NORTH DAKOTA: **Richland:** 13 mi W Walcott. OKLAHOMA: **Cimarron:** Black Mesa State Park. **Logan:** Guthrie. **Marshall:** Lake Texoma. SOUTH CAROLINA: **Beaufort:** Hilton Head Island. SOUTH DAKOTA: **Custer:** Black Hill National Forest. TEXAS: **Bastrop:** 6 mi E Bastrop. **Bosque:** Meridian State Park. **Brazos:** —. **Brewster:** 9 mi S Alpine, Big Bend National Park (Nine Point Draw). **Cameron:** Harlingen. **Colorado:** —. **Crockett:** Fort Lancaster State Historical Park. **Dallas:** Dallas. **Guadalupe:** Seguin. **Hidalgo:** Bentsen Rio Grande Valley State Park. **Hudspeth:** McNary. **Jeff Davis:** 10 and 23 mi W Fort Davis. **Kenedy:** 3 mi S Sarita. **Kimble:** Junction. **Kleberg:** Kingsville (also 20 mi SE). **Lee:** Fedor, Gidding. **Mitchell:** Lake Colorado City State Park. **Refugio:** Bayside. **San Patricio:** 8 and 10 mi NE Sinton. **Somervell:** Dinosaur Valley State Park. **Starr:** Rio Grande City, Roma. **Uvalde:** Nueces River. **Val Verde:** Amistad National Recreation Area, Del Rio, Devils River. **Victoria:** Victoria. **Webb:** 32 air mi N Laredo. **Wilbarger:** Vernon. **Williamson:** —. UTAH: **Cache:** Cornish, Logan. **Emery:** Calf Canyon (San Rafael Swell), San Rafael Desert (3 mi SSE Temple Mt.). **Garfield:** 4 mi N Boulder. **Millard:** Delta. **Uintah:** Green River 5 mi NE Jensen, 6 mi N Vernal. **Washington:** SW Bonanza, 1 mi W Leeds, Zion National Park. **Wayne:** Bullfrog Campground. WYOMING: **Platte:** Glendo.

MEXICO: **Baja California Norte:** Cataviña, 12 km NNW El Rosario (also 16 and 21 mi ESE), 4–12 mi NE El Rosarito, 1–3 and 10 mi NE Santa Rosalillita (which is 28°47′N, 114°10′W). **Baja California Sur. Chihuahua:** Ciudad Camargo, Colonia Juárez, 10–15 km S Maycoba. **Coahuila:** 61 mi N Saltillo. **Distrito Federal:** México. **Durango:** 10 mi W Durango. **Guanajuato:** 5 mi S Guanajuato. **Guerrero:** Acapulco, Chilapa, Zumpango. **Jalisco:** Chamela, Estanzuela (40 km W Ameca), 25 mi N Guadalajara, 6 mi S Ojuelos, Plan de Barrancas. **México:** Teotihuacán Pyramids. **Morelos:** 3 mi N Alpuyeca, Las Estacas. **Nayarit:** Huajicori on River Acaponeta, San Blas. **Oaxaca:** 23 mi S Matias Romero. **Puebla:** 14 mi W Huauchinango. **Querétaro:** Palmillas. **San Luis Potosí:** 20 mi E Huizache. **Sinaloa:** Chupaderos, 54 mi S Culiacán, 8 mi SE Elota, 2.5 mi S Mazatlán. **Sonora:** Alamos, Cucurpe area, La Aduana, Nogales. **Tamaulipas:** Municipio de Aldama (Rancho Nuevo), Playa Altamira. **Veracruz:** 71 mi S Panuco, Veracruz. **Zacatecas:** 10 mi S Jalpa, Rio Grande, San Juan Capistrano (22°38′N, 104°05′W).

CENTRAL AMERICA: COSTA RICA: Limón (Pulawski 1974*a*). EL SALVADOR (Pulawski 1974*a*): Los Chorros, Quezaltepeque, San Salvador. GUATEMALA: El Salto. PANAMA: Puerto Armuelles.

SOUTH AMERICA: COLOMBIA: **Magdalena:** Santa Marta (Pulawski 1974*a*). **Tolima:** Armero. VENEZUELA: **Aragua:** Lago Valencia, Ocumare de la Costa. **Falcón:** 15 km N Coro, Peninsula Paraguana (Pueblo Nuevo). **Lara:** 20 mi E Carora. **Zulia:** 6 mi W La Concepción, 10 mi E Machiques (also 31 km SW), Maracaibo, Rosario.

Tachysphex cubanus Pulawski

(Figure 49)

Tachysphex cubanus Pulawski, 1974*a*:17, ♀, ♂, ! Holotype: ♀, Cuba: Oriente Province: Ciudamar near Santiago (USNM).—Bohart and Menke 1976:273.

Diagnosis.—*Tachysphex cubanus* and *dominicanus*, the two Caribbean members of the *pompiliformis* group, share the following unique combination of characters: clypeal lobe broad, as in *antennatus* and its relatives (see Description below for details), and mesopleuron finely, evenly microsculptured, with inconspicuous, sparse punctures. The male mandible is unique within the *pompiliformis* group: the inner margin is broadly emarginate mesally (Fig. 50c). *Tachysphex cubanus* differs from *dominicanus* in having an arcuate clypeal lip in the female (without a median prominence) and an emarginate basally male forefemur. Also the gaster is differently colored: it is black basally and red apically in *cubanus*, whereas in *dominicanus* the female gaster is red except terga I–III or I–IV are black mesally, and the male gaster is black except terga I–III or I–IV red laterally.

Description.—Punctures of upper frons shallow, evanescent, several diameters apart in female, one diameter apart or less in male; averaging less than one diameter apart on vertex and scutum, but up to two or three diameters apart on scutum an-

FIGURE 49. Geographic distribution of *Tachysphex crassiformis* Viereck, *cubanus* Pulawski, and *dominicanus* sp. n.

terolaterally in female; one to two diameters apart on mesothoracic venter. Mesopleuron finely, evenly microsculptured, with sparse, inconspicuous punctures. Propodeal dorsum rugose and with ill-defined ridges, side ridged (ridges evanescent in a male from Juraguá, Cuba), hindface ridged. Discal micropunctures of tergum II two to four diameters apart. Sternum II with shallow, apical depression that is not sharply delimited anteriorly. Hindcoxa carinate basally.

Integument hidden by vestiture between antennal socket and orbit when seen from most angles. Setae inclined on mesopleuron, oriented anterad on propodeal dorsum (except basally), inclined on midfemoral venter.

Head, thorax, and legs black, or tarsal apex dark reddish; mandible yellowish red mesally. Terga I–IV (female) or I–V (male) silvery fasciate apically. Wings slightly infumate, almost hyaline. Frontal vestiture silvery.

♀.—Clypeus: bevel slightly longer to slightly shorter mesally than basomedian area; lip arcuate or weakly sinuate, incised laterally; distance between lip corners 1.7–2.0× clypeal length. Dorsal length of flagellomere I 2.0–2.25× apical width. Vertex width 0.9–1.0× length. Tergum V sparsely punctate, apical depression impunctate. Trochanteral venter minutely, closely punctate. Length 4.6–8.1 mm.

Vertex setae inclined, shorter than MOD except a few setae adjacent to orbit about 1.0 MOD long. Midscutal setae oriented obliquely posterad, but not forming well-defined pattern.

Terga I to I–III black, remainder red or (some specimens) dark, almost black; sterna red to black.

♂.—Inner mandibular margin with tooth, broadly emarginate distad of tooth. Clypeus: bevel about as long mesally as basomedian area; lip straight or sinuate, its corners well defined; distance between lip corners equal to 1.4–1.8 clypeal length. Dorsal length of flagellomere I 1.2–1.4× apical width. Vertex width 1.3–1.5× length. Sterna densely punctate throughout, punctures finer than those on mesothoracic venter. Sterna III–VI with graduli. Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II shorter than tarsomere width. Length 4.3–6.5 mm.

Vertex setae inclined or erect, shorter than MOD except a few setae adjacent to orbit about 1.0 MOD long, all setae about 1.5 MOD long in the Juraguá male; midscutal setae oriented transversely or obliquely posterad, forming a pattern.

Gaster black or (most specimens) segments IV–VI red, or all sterna brown red.

Geographic Distribution (Fig. 49).—Cuba, Jamaica.

Material Examined.—5♀, 3♂ from Cuba (paratypes); 12♀, 10♂ from Jamaica.

Records (partly from Pulawski 1974*a*).—CUBA: **Camaguey:** Camaguey. **Habana:** Cojimar. **Las Villas:** Ciénaga de Zapata. **Oriente:** Ciudamar near Santiago de Cuba, Cuabitos, Juraguá, Manicaragua, Siboney and Caney near Santiago de Cuba, Tortuguilla, Versalles near Santiago de Cuba. **Pinar del Rio:** Santa María near San Luis.

JAMAICA: **Kingston Parish:** The Palisadoes. **St. Catherine Parish:** —(Pulawski 1974*a*). **St. Thomas Parish:** Yallahs.

Tachysphex dominicanus sp. n.

(Figures 49, 50)

Derivation of Name.—Dominicanus is a neo-Latin adjective derived from dies dominica, a Sunday. The feminine gender was used to name a country, and the masculine gender is here used for the new wasp species.

Diagnosis.—*Tachysphex dominicanus* is the only member of the *pompiliformis* group found in Hispaniola. The male differs from other species of the group in having a nonemarginate forefemur (although *psilocerus* also approaches this condition). The female can be recognized by the mesopleural sculpture (integument finely, evenly microsculptured, with minute, sparse punctures; Fig. 50b) combined with the shape of clypeus (lip with obtuse median projection; Fig. 50a). The gaster color is also distinctive: in the female, the gaster is red with a black median strip on terga I–III; in the male, terga are black except terga I–III or I–IV are red laterally.

Description.—Punctures of upper frons shallow, evanescent, several diameters apart in female, one diameter apart or less in male; averaging less than one diameter apart on vertex and scutum, but up to two or three diameters apart on scutum anterolaterally in female; one to three diameters apart on mesothoracic venter. Mesopleuron finely, evenly microsculptured, with sparse, inconspicuous punctures (Fig. 50b). Propodeal dorsum microareolate and with ill-defined, longitudinal ridges; side and hindface ridged. Discal micropunctures of tergum II two to four diameters apart. Sternum II with triangular depression apically. Hindcoxa carinate basally.

Integument hidden by vestiture between antennal socket and orbit when seen from most angles. Setae: inclined or erect on vertex (shorter than MOD except a few setae adjacent to orbit about 1.0 MOD long); inclined on mesopleuron; oriented anterad on propodeal dorsum (except basally); inclined on midfemoral venter.

Head, thorax, and legs black, mandibles yellowish red mesally. Terga I–IV (female) or I–V (male) silvery fasciate apically. Wings weakly infumate, almost hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 50a): bevel equal to basomedian area or longer; lip with a median projection (projection inconspicuous in some individuals), with one or two lateral incisions; distance between lip corners 1.7–1.8× clypeal length. Dorsal length of flagellomere I 2.0–2.2× apical width. Vertex width 0.8–1.2× length. Tergum V with a few, sparse punctures, apical impression impunctate. Trochanteral venter minutely, closely punctate. Length 6.0–8.0 mm.

Midscutal setae oriented obliquely posterad, but not forming well-defined pattern.

Terga red except terga I–III or I–IV black mesally; sterna red.

♂.—Inner mandibular margin with tooth, broadly emarginate distal of tooth (Fig. 50c). Clypeus (Fig. 50c): bevel shorter than basomedian area; lip straight, weakly arcuate or weakly sinuate, its corners well defined to prominent; distance between lip corners equal to 1.4–1.5 clypeal length. Dorsal length of flagellomere I 1.2–1.5× apical width. Vertex width 1.2–1.3× length. Sterna densely punctate throughout, punctures finer than those on mesothoracic venter. Sterna III–VI with graduli. Forefemur entire. Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II shorter than tarsomere width. Length 4.3–6.5 mm.

Midscutal setae oriented transversely or obliquely posterad, forming a pattern.

Terga black except terga I–III or I–IV red laterally; sterna all or largely black.

Geographic Distribution (Fig. 49).—Eastern Cuba, Hispaniola.

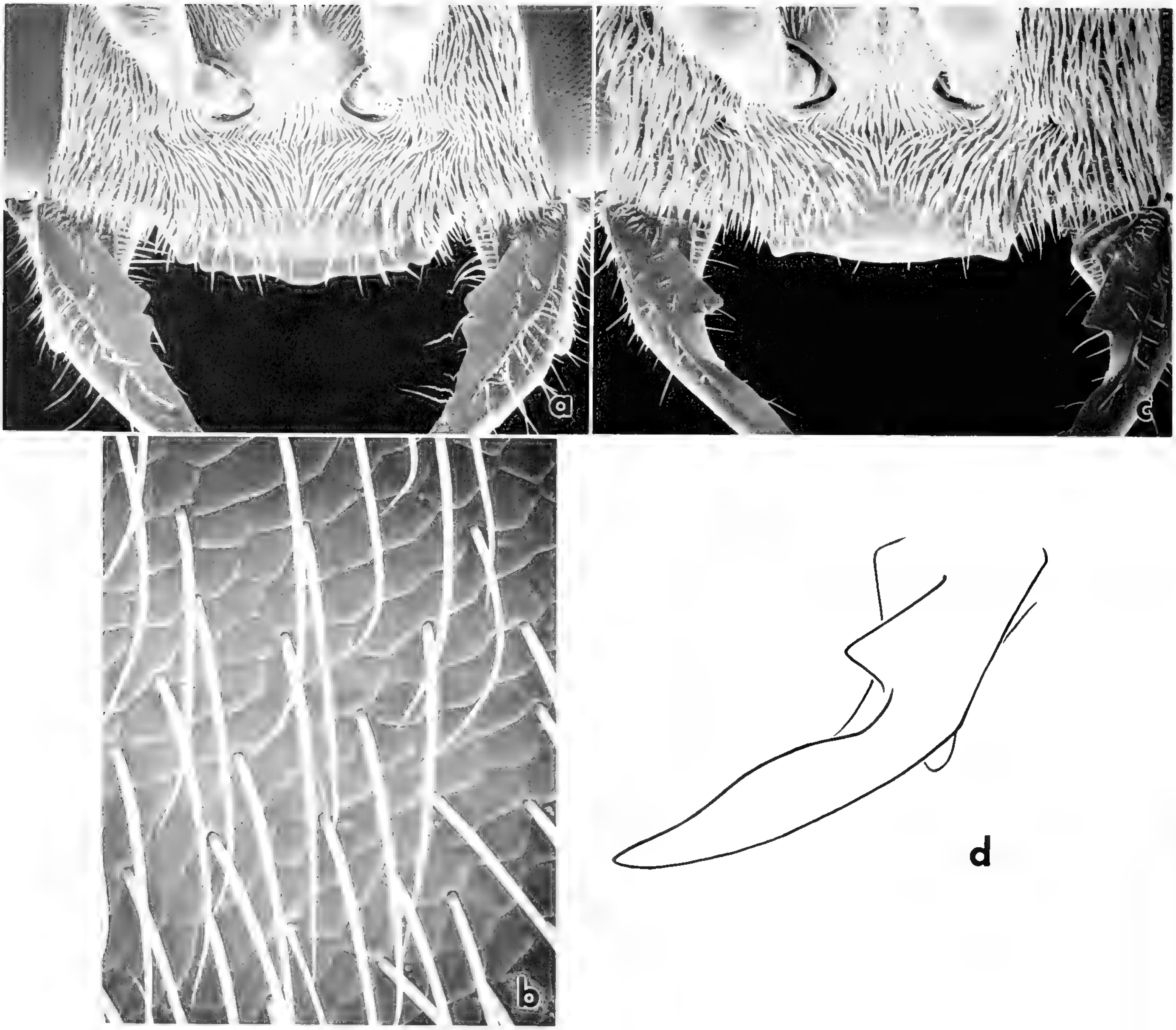

FIGURE 50. *Tachysphex dominicanus* sp. n.: a—female clypeus; b—sculpture of female mesopleuron; c—male clypeus; d—male mandible.

COLLECTING PERIOD.—May, June, September–November.

MATERIAL EXAMINED.—Holotype: ♀, Dominican Republic: Distrito Nacional, Haina, 1 Nov 1986, WJP (CAS Type #15903).

Paratypes (32♀, 33♂, specimens for which depository is not indicated are all in CAS). CUBA: **Oriente:** La Farola near Baracoa, collector unknown (1♂, paratype of *Tachysphex cubanus*).

DOMINICAN REPUBLIC: **Barahona:** Barahona, WJP (1♀, 1♂), 4 km W Barahona, WJP (2♀), 7 km E Barahona, LAS (1♀; 7♀, 6♂, FSCA), 29 km E Barahona, R. E. Woodruff and LAS (1♀, FSCA), 1.6 km W Fondo Negro, R. E. Woodruff and LAS (1♂, FSCA). **Distrito Nacional:** Haina, WJP (4♀, 4♂). **Monte Christi:** 3 km N Villa Elisa, R. E. Woodruff and LAS (1♀, FSCA); 4 km W Villa Vasquez, R. E. Woodruff and LAS (1♀, FSCA). **Pedernales:** Cabo Rojo, LAS and F. Mercano (1♀, FSCA), WJP (6♀, 13♂, 2♂, MCZ), Oviedo, WJP (2♀, 5♂). **Puerto Plata:** Playa Cabarete (32 km E Puerto Plata), WJP (1♀), Punta Rucia, R. Miller and LAS (1♀, FSCA), Sosua, WJP (1♀).

HAITI: Port-au-Prince, 10 Nov 1986, WJP (2♀).

Tachysphex paiute sp. n.

(Figures 51, 53)

DERIVATION OF NAME.—Named after the Paiute Indian group of tribes of the southwestern United States; noun in apposition.

DIAGNOSIS.—*Tachysphex paiute* is unique in having the hypostomal carina expanded into a lamella (as in *lamellatus*), with adjacent setae equal to 0.5 of mandibular basal width, and the axilla steplike or expanded and overhanging the adjacent area (as in most *crassiformis*). The shape of the male clypeus is distinctive (Fig. 51b).

DESCRIPTION.—Punctures no more than one diameter apart on frons, vertex, one to two diameters apart on scutal disk, varying from about one to two or three diameters apart on each side of mesothoracic venter. Mesopleuron dull or shiny, with

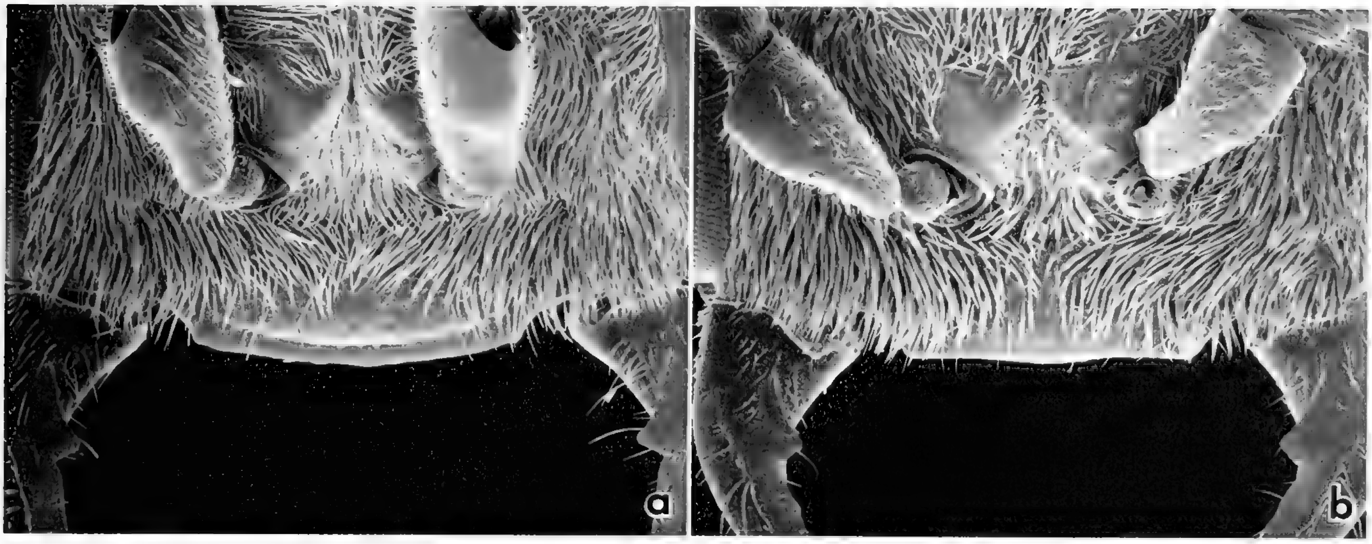

FIGURE 51. *Tachysphex paiute* sp. n.: a—female clypeus; b—male clypeus.

well-defined punctures that are less than one to more than one diameter apart. Propodeal dorsum areolate, side ridged (weakly so in two of the three males examined), hindface ridged. Sternum I with apical depression. Hindcoxa carinate basally.

Setae concealing integument between antennal socket and orbit; suberect to subappressed on vertex, suberect on mesopleuron, oriented anterad on propodeal dorsum mesally, subappressed on midfemoral venter; setae adjacent to hypostomal carina as long as 0.5 of basal width of mandible; midscutal setae oriented obliquely posterad to nearly laterad.

Head, thorax, and legs black or apical tarsomeres reddish. Gaster red; terga I–IV (I–V in male) silvery fasciate apically. Frontal vestiture silvery. Wings hyaline.

♀.—Clypeus unusually broad (Fig. 51a): distance between lip corners 1.8–2.2× clypeal midline, and 1.6–1.7× distance between lip corner and orbit; free margin of lip almost straight, without median notch or lateral incision; bevel shorter than basomedian area. Dorsal length of flagellomere I 2.5–2.8× apical width. Vertex width 0.9–1.1× length. Discal micropunctures of tergum II several diameters apart. Tergum V sparsely punctate, apical depression impunctate. Pygidial plate alutaceous, sparsely punctate. Mid- and hindtrochanteral venter sparsely punctate (sparsely punctate area evanescent in one female from Antelope Springs). Femora densely microsculptured, but sculpture evanescent near base. Length 7.0–7.7 mm.

♂.—Mandibular inner margin with tooth (Fig. 51b). Clypeus (Fig. 51b): free margin of lobe nearly straight; lobe corners well defined, 1.4× as far from each other as corner is from orbit and 2.2× clypeal length; lip not or scarcely differentiated from bevel; the latter markedly shorter than basomedian area. Dorsal length of flagellomere I 2.1–2.3× apical width. Vertex width 1.3–1.6× length. Sterna uniformly punctate or sterna II and III largely impunctate mesally; punctures finer than those of mesothoracic venter. Forefemoral notch with conspicuous setae. Forebasitarsus with two or three preapical rake spines. Outer apical spine of foretarsomere II slightly longer than tarsomere width. Length 5.0–6.0 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 53).—Death Valley area in California to Baja California Sur, Mexico.

COLLECTING PERIOD.—30 March to 1 April (Baja California), 17 April to 4 June (California).

MATERIAL EXAMINED.—Holotype: ♀, California: Inyo Co.: Antelope Springs, 24 Aug 1960, PDH (CIS, on indefinite loan to CAS, CAS Type #15907)

Paratypes (5♀, 3♂): UNITED STATES: CALIFORNIA: **Imperial:** Chocolate Mts., Ogilby Road 3 mi S junction Highway 78, 16–22 Oct 1977, MSW (1♀, CSDA). **Inyo:** same data as holotype (1♀, CIS); Eureka Valley, May 1978, D Giuliani, A. Hardy, F. G. Andrews (1♂, CSDA); Eureka Valley, 12 mi N 10 mi W Sand Dunes, 6 May–4 June 1979, D. Giuliani (1♂, CSDA); Little Lake, 20 May 1951, EIS (1♀, UCD; gaster missing); Owens Lake Valley, 17 Apr–18 May 1978, F. G. Andrews, A. Hardy, D. Giuliani (1♂, CAS)

MEXICO: **Baja California Sur:** 35 km S Mulegé, L. D. French and E. A. Sugden, 30 Mar 1980 (1♀, CAS), 1 Apr 1980 (1♀, UCD)

Tachysphex pinal sp. n.

(Figures 52, 53)

DERIVATION OF NAME.—Named after the Pinal Apache Indians of Arizona; a noun in apposition. Also an allusion to Pinal County and the mining town of Pinal, now the site of Boyce Thompson Arboretum, where the holotype was collected.

DIAGNOSIS.—*Tachysphex pinal* has an unusually broad clypeal lobe (Fig. 52a, b): the distance between the corners equals 1.7–1.9× clypeal length in the female and 1.5–1.6 in the male. The clypeus is also unusually broad in *antennatus, crassiformis, krombeini, paiute,* and *toltec,* but the erect vertex setae of *pinal* separate it from all these species except *toltec.* Other important characters are: axilla evenly rounded (axilla expanded or steplike in *paiute* and most *crassiformis*), midscutal setae oriented laterad or nearly so, forming a conspicuous pattern (scutal setae oriented posterad in *antennatus*). In the female, the vertex width is 1.0–1.1× length and the gaster is all red (in the female of *toltec,* the vertex width is 1.3–1.5× length, and the gaster is black basally and red apically). In the male, the preapical flagellomeres are the usual length, and the forefemoral notch is the usual size (the preapical flagellomeres of *toltec* are unusually short, Fig. 54c, and the forefemoral notch is unusually large,

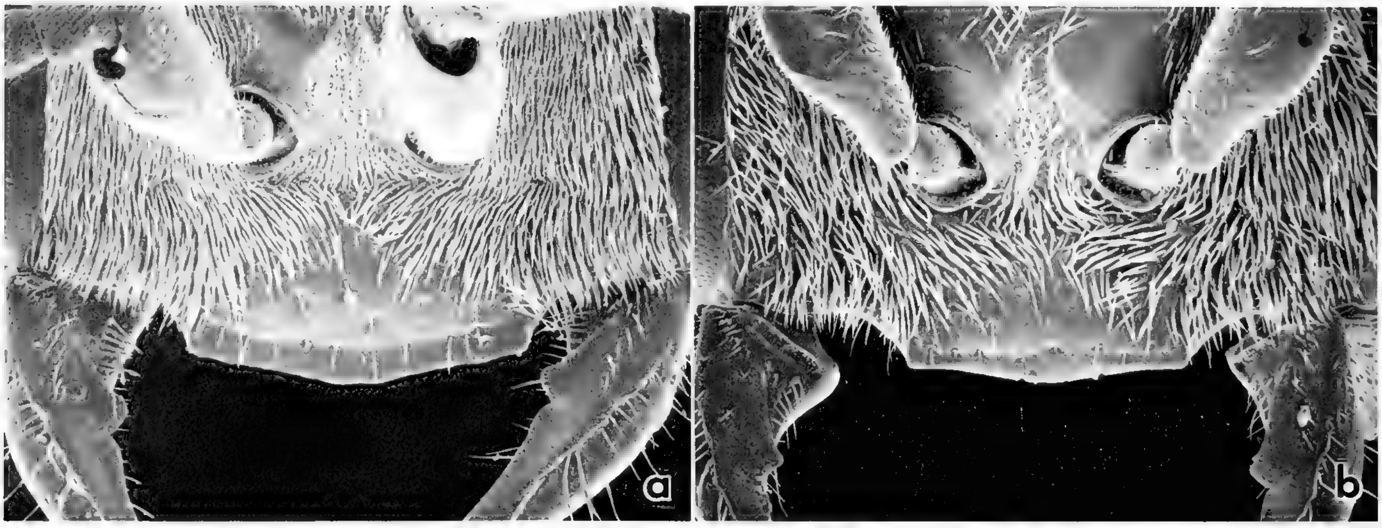

FIGURE 52. *Tachysphex pinal* sp. n.: a—female clypeus; b—male clypeus.

Fig. 54d). An undescribed phenon from southern California and Nevada resembles *pinal* in the shape of clypeus and in having erect vertex setae, but unlike *pinal* its scutal setae are oriented uniformly posterad.

DESCRIPTION.—Punctures averaging about one diameter apart on frons, varying from about one to several diameters apart on vertex; up to two or three diameters apart on mesothoracic venter; on scutum, largest interspaces between punctures varying from about one (some females, many males) to many puncture diameters. Propodeal dorsum microareolate, slightly sloping apically toward transverse carina that separates it from hindface; side finely, densely ridged; hindface ridged. Micropunctures of tergum II several (female) to few (male) diameters apart. Sternum II at most with ill-defined apical depression. Hindcoxa carinate (carina not expanded into tooth).

Integument hidden by vestiture between antennal socket and orbit. Setae erect, about 1.5 MOD long, on vertex; about 1.0 MOD long and oriented transversely on midscutum (or anterolaterad, or posterolaterad, or radially in some specimens); inclined on mesopleuron; oriented anterad on propodeal dorsum along midline; nearly appressed on midfemoral venter.

Head, thorax, and legs black; mandible reddish yellowish mesally; apical tarsomeres brown. Gaster all red (female) or (most males) three or four apical segments black; gaster all black in the only male examined from Wyoming. Terga I–IV (female) or I–V (male) silvery fasciate apically; apical fascia broadly interrupted mesally. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 52a): bevel as long mesally as basomedian area or longer; lip weakly sinuate, incised laterally in most specimens, but entire in some; distance between lip corners 1.7–1.9 × clypeal length. Dorsal length of flagellomere I 2.0–2.2 × apical width. Vertex width 1.0–1.1 × length. Tergum V sparsely punctate, apical depression impunctate. Trochanteral venter minutely, closely punctate. Length 7.0–8.0 mm.

♂.—Inner mandibular margin with tooth (Fig. 52b). Clypeus (Fig. 52b): bevel shorter than basomedian area; lip straight, arcuate, or weakly sinuate, its corners well defined to prominent; distance between lip corners equal to 1.5–1.6 clypeal length. Dorsal length of flagellomere I 1.6–2.0 × apical width. Vertex width 1.5–1.8 × length. Sterna densely punctate throughout, punctures finer than those on mesothoracic venter. Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II shorter than tarsomere width. Length 5.0–6.0 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 53).—Southwestern Wyoming, Utah, Arizona, New Mexico, southwestern Texas, California, and Baja California, and State of Sonora in Mexico; xeric habitats.

COLLECTING PERIOD.—24 February (Sonora, Mexico), 17 March (Baja California) to 2 July (Wyoming).

MATERIAL EXAMINED.—Holotype: ♀, Arizona: Pinal Co.: Boyce Thompson Arboretum 3 mi W Superior, 26 May 1985, WJP (CAS, Type #15912).

Paratypes (47♀, 87♂): UNITED STATES: ARIZONA: **Cochise:** Portal, 23 Apr 1985, WJP (1♀, 2♂, CAS), 14 mi W Tombstone, 16 Apr 1965, FDP (1♀, 2♂, BMNH; 2♀, 2♂, CAS; 10♀, 39♂, UCD; 1♀, 2♂, USNM); 2 mi E Texas Canyon, 11 May 1985, A. D. Telford (2♀, UCD); 3 mi E Willcox, 17 Apr 1986, WJP (1♂, CAS). **Coconino:** Antelope Hills [locality not found on available maps], 10 May 1978, R. C. Miller (1♂, UCD). **Graham:** Roper Lake State Park, 15 Apr 1986, WJP (1♀, CAS). **Mohave:** Wikieup, 18 May 1986, WJP (1♀, CAS). **Pima:** 8 mi SE Continental, 2 Apr 1986, TLG (1♂, USU); Sabino Canyon in Santa Catalina Mountains, 6 Apr 1957, G. Butler and F. Werner (1♀, UCD); 27 mi SE Tucson, 29 May 1965, MEI (1♀, UCR). **Pinal:** same data as holotype (3♀, CAS). **Santa Cruz:** 5 km W Arivaca Junction, 2 Apr 1986, TLD (1♂, CAS); 12 mi SW Patagonia, 22 Apr 1985, WJP (1♂, CAS). CALIFORNIA: **El Dorado:** 3 mi S Camino, 26 June 1948, JWMS (1♀, UCD). **Inyo:** 3 mi W Lone Pine, 15 May 1970, RMB (1♀, UCD). **Placer:** Martis Valley, 1 July 1964, FDP (1♀, UCD). **Riverside:** 5 mi N Blythe, 24 March 1968, D. S. Horning (1♂, UCD); Chino Canyon 3 mi W Palm Springs, 30 March 1970, EEG and R. F. Denno (1♂, UCD). **San Bernardino:** 4 mi S Baker, 23 Apr 1969, MSW and J. S. Wasbauer (2♂, CSDA); 8 mi NE Cima, 19 May 1986, WJP (1♂, CAS); Granite Mountains, 9 June 1980, TLG (TLG), 12 mi SE Ivanpah, 1 May 1956, PDH (1♀, 11♂, UCD); 7 mi SW Kelso, 16 Apr 1969, MSW and J. S. Wasbauer (1♂, CAS; 2♂, CSDA); Providence Mountains State Park, 28 May 1985, WJP (6♀, 2♂, CAS). NEW MEXICO: **Catron:** Glenwood, 1 June 1965, RMB (1♀, UCD). **Lincoln:** Valley of Fires State Park, 22 May 1985, WJP (1♂, CAS). **Sierra:** Percha Dam State Park, 21 Apr 1986, WJP (1♂, CAS). TEXAS (all 1986, TLG): **Brewster:** Big Bend National Park: Government Spring, 13 Apr (2♀, USU). Oak Creek, 14 Apr (1♀, USU). **Culberson:** 26 km N Van Horn, 9 Apr (1♀, 3♂, CAS; 1♀, 3♂, USU); Guadalupe National Park (SE corner), 7 Apr (1♀, USU), Guadalupe National Park (junction of Highway 62 and McKittrick Canyon Road), 8 Apr (1♂, CAS). UTAH: **Carbon:** Price, 26 May 1967, G. F. Knowlton (1♀, USU). **Washington:** Paradise Canyon, 24–28 May 1983, Dan Beck (2♂, CAS, USU). WYOMING: **Sweetwater:** Green River, 2 July 1920, collector unknown (1♀, UCD).

MEXICO: **Baja California Norte:** 21 mi ESE El Rosario, 17 Mar 1984, WJP (1♂, CAS). **Baja California Sur:** 30 mi ESE Bahía Tortugas, 26 Mar 1984 (1♀,

CAS); eastern edge of Sierra Placeres, 27°35'N, 114°30'W, 24 Mar 1984, WJP (1♂, CAS). **Sonora:** Alamos, 24 and 26 Feb 1963, PHA (2♂, CAS).

Tachysphex toltec sp. n.

(Figures 53, 54)

Derivation of Name.—Named after the Toltec Indians of Mexico whose capital was Teotihuacán (where the holotype was collected); noun in apposition.

Diagnosis.—Like *pinal, toltec* has a broad clypeal lobe (distance between lip corners equal to 1.7–1.8 clypeal length in the female and 1.4–1.5 in the male; Fig. 54a, b) and erect vertex setae. The female of *toltec* can be recognized by the characters given under *pinal* (page 81). In the male, the apical flagellomeres are shorter than in other species (Fig. 54c); for example, the maximum length : maximum width ratio of flagellomere VIII is about 1.1 in *toltec,* about 1.5–1.9 in *antennatus,* and 1.8 in *crassiformis.* Another diagnostic feature of the male is its unusually deep, densely pubescent forefemoral notch (Fig. 54d, e).

An undescribed phenon from central and southern Mexico resembles *toltec* in size, sculpture, and pilosity (some specimens were also collected in Teotihuacán). Unlike *toltec,* the female has nearly appressed vertex setae and an all black gaster; in the male, the apical flagellomeres are not shortened, and the forefemoral notch is smaller and shallower; in both sexes, the corner of the clypeal lobe is less prominent than in *toltec.*

Description.—Punctures nearly contiguous on frons; in most specimens averaging no more than one diameter apart on vertex, scutum and mesothoracic venter, but averaging one to two diameters apart on vertex and scutal disk in a female from Durango area. Mesopleuron dull, microsculptured, with shallow, inconspicuous punctures. Propodeal dorsum microareolate, sloping toward transverse carina that separates it from hindface; side dull, microareolate, in most specimens microridged when seen from certain angles; hindface ridged or (some males) ridges evanescent. Discal micropunctures of tergum II several (female) or few (male) diameters apart. Sternum I at most with ill-defined apical depression. Hindcoxa carinate basally.

Integument hidden by vestiture between antennal socket and orbit as examined from most angles. Setae erect, 1.0 MOD long, on vertex; oriented transversely on midscutum; inclined on mesopleuron; on propodeal dorsum inclined anterolaterad or (some males) oriented anterad along midline; on midfemoral venter in apical half almost appressed (female) or almost erect (male).

Head, thorax, and legs black, tarsal apex brown. Terga I–III silvery fasciate apically. Wings weakly infumate (female) or nearly hyaline (male). Frontal vestiture silvery.

♀.—Clypeus (Fig. 54a): bevel mesally longer than basomedian area; lip weakly sinuate, excised laterally; distance between lip corners 1.7–1.8× clypeal length. Dorsal length of flagellomere I 1.9–2.0× apical width. Vertex width 1.3–1.5× length. Tergum V sparsely punctate mesally, apical depression impunctate. Trochanteral venter closely punctate. Forebasitarsus with six rake spines; only two apical spines with confluent basal fossae. Length 7.0–7.5 mm.

Gastral segment I black, II–IV black or largely red, V and VI red.

♂.—Inner mandibular margin with tooth (Fig. 54b). Clypeus (Fig. 54b): bevel shorter than basomedian area; lip nearly straight, with prominent corners that are separated by a distance equal

Figure 53. Geographic distribution of *Tachysphex paiute* sp. n., *pinal* sp. n., and *toltec* sp. n.

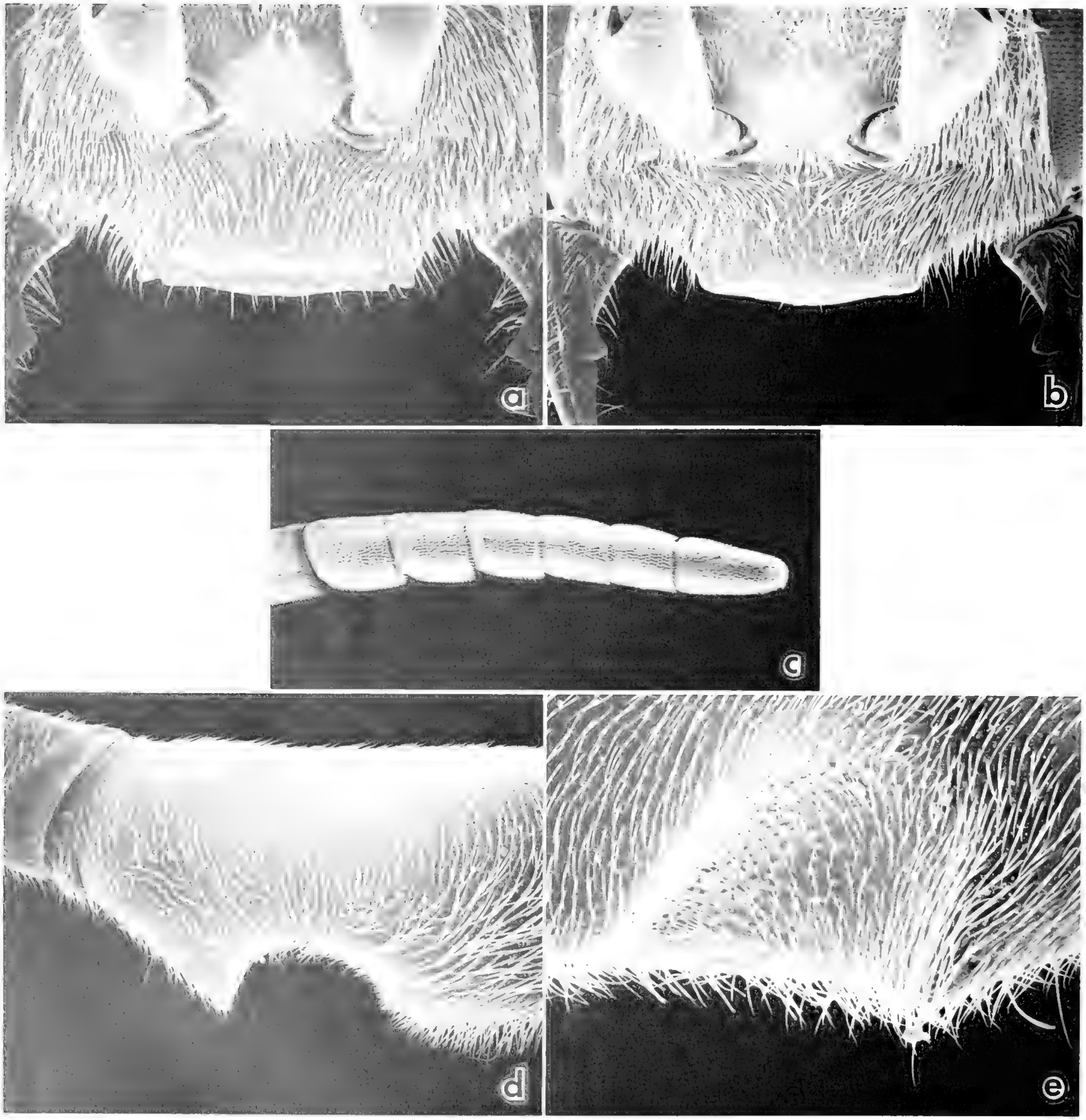

FIGURE 54. *Tachysphex toltec* sp. n. a—female clypeus. b—male clypeus. c—apical flagellomeres of male; d—forefemoral notch of male; e—surface of the forefemoral notch.

to 1.4–1.5 of clypeal length. Dorsal length of flagellomere I 1.4–1.7 × apical width. Apical flagellomeres (Fig. 54c) shorter than in other species (e.g., maximum width:length ratio of flagellomere VIII is about 1.1). Vertex width 1.7–1.9 × length. Sterna densely punctate throughout, punctures finer than those on mesothoracic venter. Forefemoral notch deep (about one-third of femoral diameter), covered with dense, conspicuous pruinosity (Fig. 54d, e). Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II markedly shorter than tarsomere width. Length 5.3–6.7 mm.

Gastral segments IV–VII dark, tergum I partly black (almost entirely in some specimens), remainder red or partly black.

GEOGRAPHIC DISTRIBUTION (Fig. 53).—Central Mexico.

COLLECTING PERIOD.—17 June to 26 July.

MATERIAL EXAMINED.—Holotype ♂, Mexico: Mexico State, Teotihuacán pyramids, 15 June 1951, PDH (CIS, on indefinite loan to CAS, CAS Type #15909).

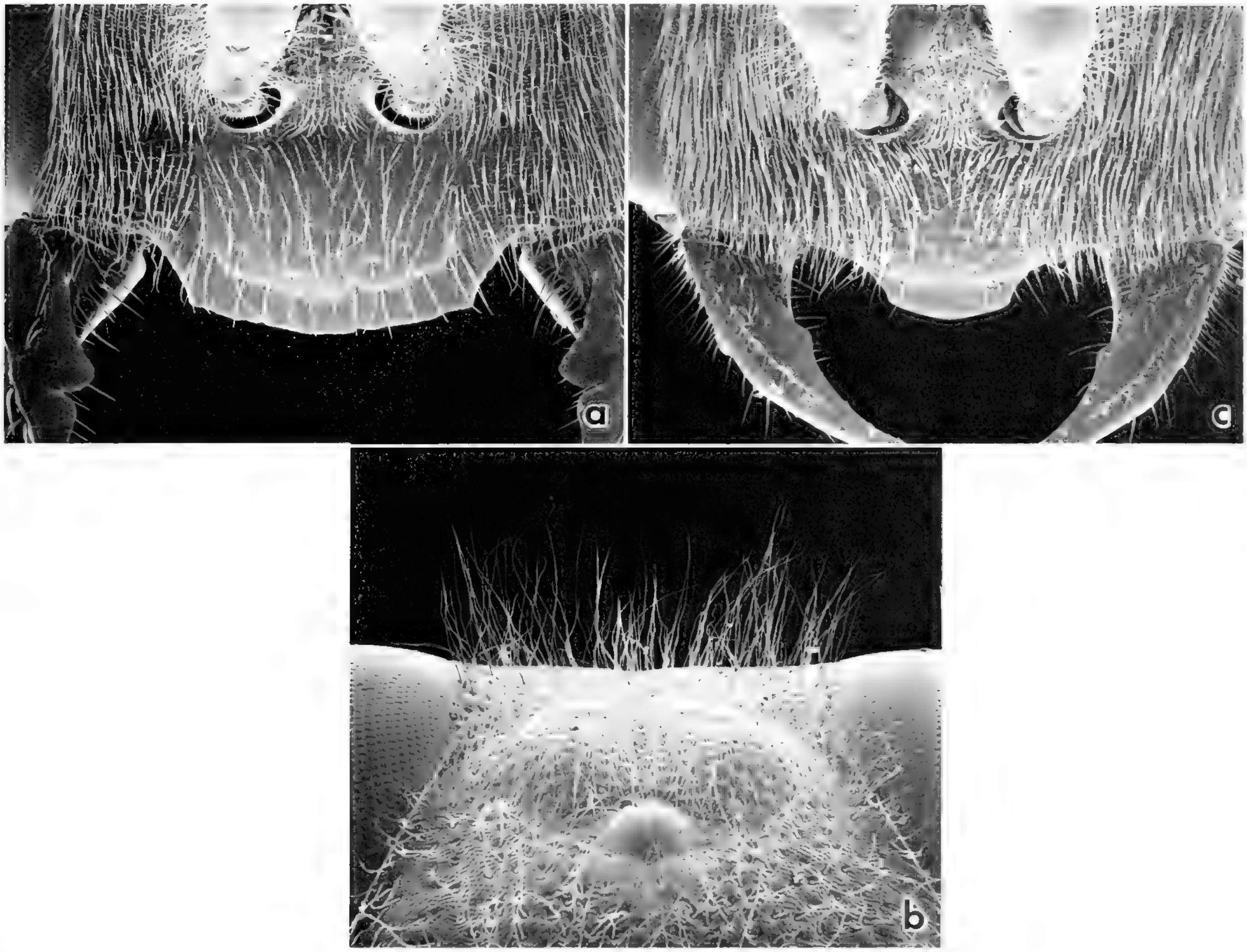

FIGURE 55. *Tachysphex idiotrichus* Pulawski: a—female clypeus; b—female vertex; c—male clypeus.

Paratypes (3♀, 8♂): MEXICO: **Durango:** 7 mi W Durango, 26 July 1964, W. R. Mason (1♀, CNC); 10 mi W Durango, 12 July 1954, JWMS (1♀, 1♂, CIS). **Jalisco:** 40 mi W Guadalajara, 18 June 1963, H. A. Scullen and D. D. Bollinger (1♀, OSU). **México:** same data as holotype (1♀, 2♂, CAS; 5♂, CIS).

Tachysphex idiotrichus Pulawski

(Figures 55, 56)

Tachysphex idiotrichus Pulawski, 1982:31, ♀, ♂. ! Holotype: ♀, Arizona: Cochise Co.: Southwestern Research Station 5 mi W Portal (UCD)

DIAGNOSIS.—*Tachysphex idiotrichus* differs from other North American species of the *pompiliformis* group in having unusually long setae on the head (Fig. 55b), thorax, and femora; the large punctures on the middle section of the female clypeus (also basally); the presence of graduli on sterna III–V of the female; and the sparsely punctate (except apex) male tergum VII. Subsidiary diagnostic characters are: sparsely punctate vertex; and in the male, vertex width more than twice length (like *pechumani*), presence of graduli on sterna III–VI (like *ashmeadii, glabrior, irregularis,* and *verticalis*), and compressed forefemoral notch (like *apricus*).

DESCRIPTION.—Frons dull, strongly microreticulate, with shallow punctures that are less than one diameter apart. Vertex and scutal disk microreticulate, punctures averaging two to four diameters apart (but subcontiguous on vertex anteriorly). Mesopleuron dull, strongly microareolate, with shallow, inconspicuous punctures that are more than one diameter below scrobe, irregularly rugose above in some individuals. Propodeal dorsum microareolate, side and hindface ridged (side ridges partly evanescent in male). Sterna III–V (also VI in male) with graduli. Hindcoxa carinate basally.

Head, thorax, and legs black. Tergum I black (except usually red apically), remaining terga red. Sternum I black, sterna II–V black mesally, remainder red (red zone small on sternum II but large on V). Terga I–III (also IV in male) weakly, silvery fasciate apically. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 55a): middle section with large punctures, shiny apically, dull, microreticulate basally; lip without mesal notch or lateral indentations; several punctures of lateral section more than one diameter apart. Dorsal length of flagellomere I 2.6–3.0 × apical width. Vertex width 1.3–1.5 × length. Punctures of mesothoracic venter mostly close to each other, but averaging two to three diameters apart in California specimens. Micropunctures of tergum II several diameters apart posteromedially,

FIGURE 56. Geographic distribution of *Tachysphex idiotrichus* Pulawski.

absent on apical depression; tergum V usually with a few, sparse punctures, but densely punctate (except medially) in some specimens. Trochanteral venter alutaceous, punctate; forefemoral venter strongly microsculptured, with shallow, indistinct punctures. Length 10.0–10.5 mm.

Vestiture not obscuring integument between antennal socket and orbit. Setal length (in MOD): 2.0–2.5 on outer face of scape, 2.5–3.0 on vertex (Fig. 55b), 2.5 on lower gena, 2.0 on scutum anteriorly and on midfemoral venter (sometimes only a few midfemoral setae are this long).

♂.—Mandibular inner margin with obtuse tooth (Fig. 55c). Clypeus (Fig. 55c): bevel much shorter than basomedian area; lip arcuate, its corners indistinct, more than twice closer to each other than to orbits. Dorsal length of flagellomere I 1.9–2.2× apical width. Vertex width about 2.3× length. Tergum V with a few, sparse punctures, except densely punctate apically. Most punctures of sterna III–VI more than one diameter apart. Forefemoral notch compressed, so that its glabrous bottom forms an obtuse, longitudinal crest. Forebasitarsus with up to five preapical spines that are equal to forebasitarsal width or slightly longer. Outer apical spine of foretarsomere II as long as foretarsomere III. Length 7–8 mm.

Vestiture obscuring sculpture between antennal socket and orbit when seen from some angles. Setal length (in MOD): 1.5–2.0 on outer face of scape, 2.2–3.0 on vertex, 1.5–2.0 on lower gena and scutum anteriorly, 1.0–2.0 on midfemoral venter.

GEORAPHIC DISTRIBUTION (Fig. 56).—Low mountain areas of southwestern Texas, New Mexico, Arizona, and southern California south to Jalisco State, Mexico.

MATERIAL EXAMINED.—25♀, 11♂ (AMNH, BMNH, CAS, CSU, TLG, UAE, UAT, UCD, USNM).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** 3 mi E Apache, 2 mi W Chiricahua National Monument, 2 mi SW Portal (also 5 mi W), Sulphur Spring Valley, 14 mi W Tombstone, 1 mi SE Willcox. **Pima:** Tucson. **Yavapai:** Cottonwood (also 7 mi N). CALIFORNIA: **San Bernardino:** Mid Hills (9 mi SSE Cima). NEW MEXICO: **Hidalgo:** Rodeo to Road Forks. **Otero:** Alamogordo. **Socorro:** 10 mi W Socorro. TEXAS: **Pecos:** —

MEXICO. **Jalisco:** Lagos de Moreno

Tachysphex tahoe sp. n.

(Figures 57, 58)

DERIVATION OF NAME.—Tahoe is a Washo Indian name meaning big water; noun in apposition. An allusion to the type locality which is in the Lake Tahoe area.

DIAGNOSIS.—Females of *tahoe* have ill-defined mesopleural punctures (Fig. 57b, c), inclined hypoepimeral setae, and the clypeal lip is entire (Fig. 57a). This combination is also found in *apricus, occidentalis,* and *solaris,* but their femora and tibiae are all or partly red (see these species for further differences). In *tahoe,* the femora and tibiae are black. Also, the setae of the propodeal dorsum of *tahoe* are inclined anterolaterad in dorsal view and anterad in lateral view (erect or nearly so in *semirufus*), the mesopleural setae are shorter and more inclined than in *semirufus,* and terga I–IV of most specimens are weakly fasciate apically (not fasciate in *semirufus*). The clypeal lip is weakly sinuate, Figure 57a (evenly arcuate in *miwok*), and the vertex setae are erect, possibly with exceptions (appressed in *miwok*).

In the male of *tahoe,* sterna III–VI are velvety pubescent, the clypeal lip is triangular (Fig. 57d), the inner mandibular margin is not dentate (Fig. 57d), and the mesopleuron lacks well-defined punctures. *Tachysphex musciventris* shares these features, but in *tahoe* hypoepimeral setae are inclined, and pubescence of sternum II is not velvety, not obscuring integument, thus contrasting with the following sterna. In addition, the vertex width equals 1.1–1.4× length in *tahoe* and 1.3–2.0× in *musciventris.*

DESCRIPTION.—Punctures subcontiguous on frons, scutum, and mesothoracic venter, no more than one diameter apart on ver-

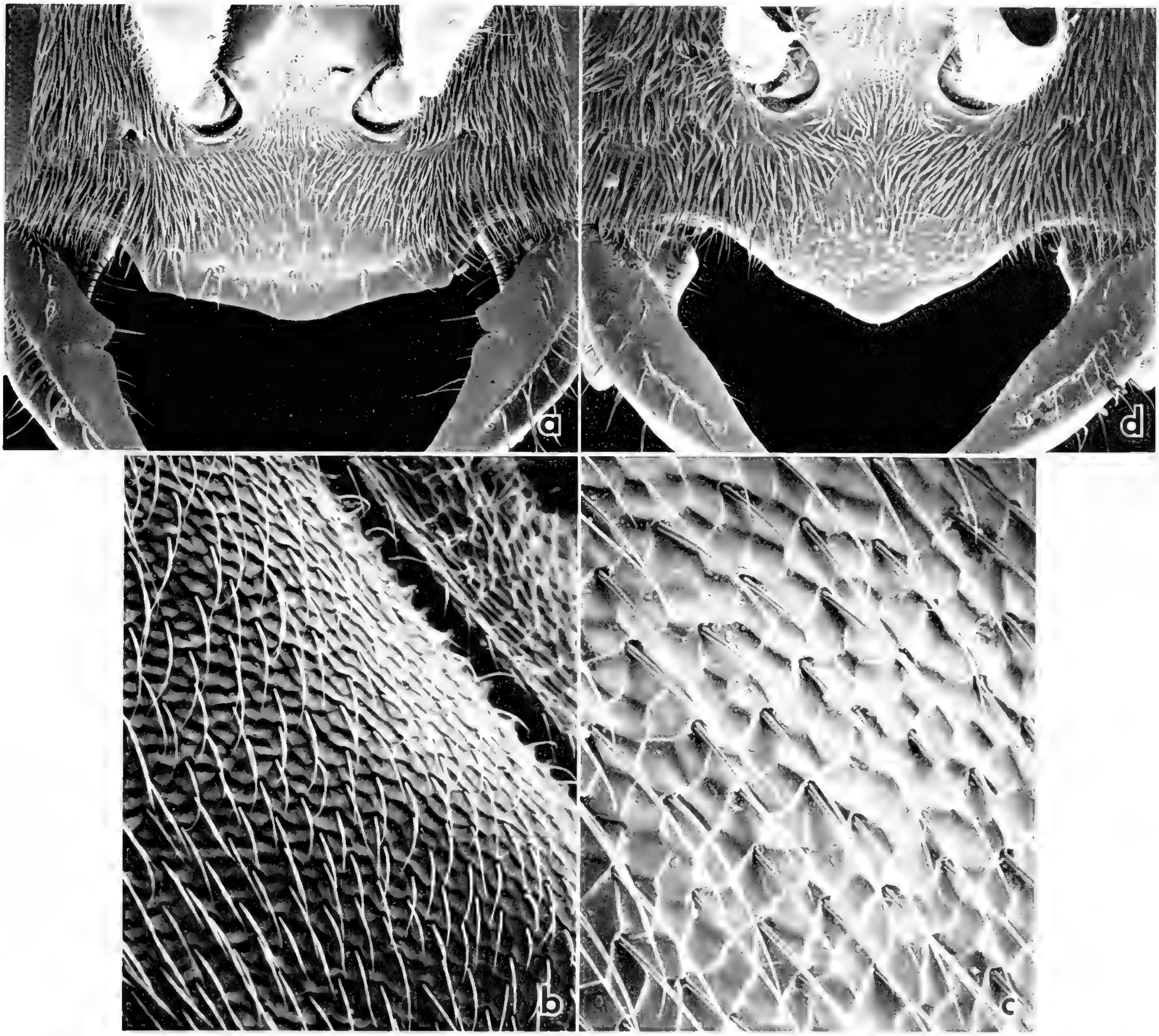

FIGURE 57 *Tachysphex tahoe* sp. n.: a—female clypeus; b—sculpture of female mesopleuron; c—same, different angle; d—male clypeus

tex. Mesopleuron dull, irregularly microsculptured, its punctures ill defined, shallow, subcontiguous (Fig. 57b, c). Propodeal dorsum and side microareolate, side of most specimens microridged when seen from certain angles; hindface finely ridged. Discal micropunctures of tergum II varying from one or two to about three or four diameters apart. Sternum I with shallow apical depression. Hindcoxa not carinate.

Vestiture totally obscuring integument between antennal socket and orbit. Setae erect, about 1.0 MOD long, on vertex (appressed in some males); midscutal setae oriented posterolaterad or (some females) transversely; suberect on hypoepimeral area; subappressed beneath mesopleural scrobe; oriented anterolaterad on propodeal dorsum except oriented posterad basally; appressed or nearly so on midfemoral venter.

Head and thorax black, gaster red or (some males) segments IV–VII brown. Legs black, tarsal apex reddish. Terga I–IV silvery fasciate apically (weakly so in female), not fasciate in single female from Aguanga area, California. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 57a): middle section almost flat; bevel longer than basomedian area; lip scarcely sinuate, obtusely angulate mesally, not incised laterally; free margin shallower between lip and orbit than in *antennatus* or *tarsatus* (Fig. 57a). Dorsal length of flagellomere I 1.8–2.6 × apical width. Vertex width 0.9–1.1 × length. Tergum V with a few, sparse punctures, apical depression impunctate. Punctures of mid- and hindtrochanteral venter minute, several diameters apart. Length 6.5–8.0 mm.

♂.—Inner mandibular margin not dentate (Fig. 57d). Clypeus (Fig. 57d): bevel much shorter than basomedian area; free margin not angulate to moderately angulate between lobe and lateral section; lip obtusely triangular, of varying width (see Variation below). Dorsal length of flagellomere I 1.5–2.0 × apical width.

FIGURE 58. Geographic distribution of *Tachysphex tahoe* sp. n.

Vertex width 1.1–1.4 × length. Sternal punctures finer than those of mesothoracic venter. Forefemoral notch shiny, glabrous. Forebasitarsus usually without preapical rake spines, occasionally with one such spine; outer apical spine of foretarsomere II shorter than foretarsomere III. Length 5–8 mm.

Sterna II–VI velvety pubescent (except on apical depressions).

VARIATION.—Distance between clypeal lip corners in most males less than distance between corner and orbit and equal to 0.9–1.0 clypeal length. In coastal individuals (San Luis Obispo and San Diego counties of California), distance between lip corners is more than distance between corner and orbit, and equal to 1.2 of clypeal length. Vertex setae in most specimens erect, about 1.0 MOD long, but appressed in coastal males.

LIFE HISTORY.—Several females and males from Boca, California have been collected on flowers of *Eriogonum*. A female from Frazier Mountain area, California, was collected on flowers of *Baeria chrysostoma* F. and M.

GEOGRAPHIC DISTRIBUTION (Fig. 58).—California, Nevada, southeastern Arizona, and Baja California (Norte), mainly montane areas.

COLLECTING PERIOD.—17–19 March (central Baja California), 18 April to 16 September (United States).

MATERIAL EXAMINED.—Holotype: ♂, California: Placer Co.: Carnelian Bay on Lake Tahoe, 4 July 1958, RMB (UCD).

Paratypes (88♀, 84♂; specimens for which depository is not indicated are all in UCD): UNITED STATES: ARIZONA: **Cochise:** Portal, WJP (5♂, CAS). CALIFORNIA: **Alpine:** Fredericksburg, WWM (1♀); Indian Creek Lake, GEB (1♀, USU). **El Dorado:** Icehouse Road (24 air mi ENE Placerville), WJP (1♀, CAS). **Fresno:** Auberry, J. A. Halstead (1♀, CAS); 12 mi SE Shaver Lake, J. A. Halstead (2♂, CAS). **Inyo:** Argus Mts., C. D. Michener (1♀, KU); Big Pine, RMB (1♀); 9 mi W Lone Pine, RMB (1♀); Lone Pine Creek, TLG (1♀, TLG). **Kern:** Short Canyon, R. O. Schuster (1♀, UCD). **Lake:** Hopland Grade, S. M. Fidel (1♀). **Lassen:** Hallelujah Junction, RMB, J. Slansky (2♀, 1♂), Summit Camp, EGL (3♀). **Los Angeles:** Crystal Lake, HEE (1♀, UCD), 2.5 mi S Pearblossom, R. W. Brooks (1♀, UCD). **Marin:** Alpine Lake, J. M. Burns (1♀, CIS). **Modoc:** Cedar Pass Campground, PHA (2♀, CAS). **Mono:** 11 mi N Bridgeport, PMM (1♀); Paradise Camp, ASM (2♀, 2♂; 1♀, WJP), Sweetwater Mts., S Fork Cottonwood Creek, HKC (1♀). **Napa:** 5.5 km NW Moscowite Corner (Capell Creek), PHA (1♀, CAS). **Nevada:** Boca, RMB, EEG, MEI, PMM, WJP, EIS, LAS (3♀, CAS; 19♀, 13♂; 3♀, 2♂, USNM; 2♀, 4♂, WJP); Prosser Dam, D. R. Miller (1♂); Sagehen Creek near Hobart Mills, MEI, FDP (1♀, 2♂). **Placer:** Carnelian Bay on Lake Tahoe, RMB (1♀, 1♂); Emigrant Gap (27 air mi W Truckee), WJP (4♀, 15♂, CAS), 4 air mi S Soda Springs, WJP (2♂, CAS); 7 mi SE Truckee, RMB (1♀). **Plumas:** 6 mi E Chester, G. Schaefers (1♀); Little Long Valley Creek (6 mi E Spring Garden), MSW (1♀, CSDA). **San Bernardino:** 2 mi W Cajon Pass, EIS (1♂); Holcomb Valley, KWC (1♀, CAS); Granite Mts., TLG (1♂, TLG), Indian Cove in Joshua Tree National Monument, KWC (2♀, 1♂, CAS), K. V. Krombein (1♀, 2♂, USNM); Vidal Junction, EGL (1♀); Willow Wash, TLG (1♂, CAS). **San Diego:** 11 mi W Aguanga, EIS (1♀, UCD); Anza Borrego Desert State Park (Plum Canyon at Yaqui Flat), K. V. Krombein (1♂, USNM); Borrego, PDH (1♀), Sorrento Beach, JAP (1♂, CIS). **San Luis Obispo:** Dune Lakes (3 mi S Oceano), J. Doyen, P. Rude (1♂, CIS), JAP (1♂, CIS). **Santa Barbara:** Santa Ynez Mts., FDP (1♂). **Sierra:** Sardine Lakes, no collector (1♀); Sierraville, RMB (1♀, CAS, 1♀, 1♂). **Siskiyou:** 1 mi SW McCloud, WJP (1♀, CAS); 27 road mi NE Weed, WJP (1♀, CAS). **Tulare:** Ash Mt. near Kaweah Power Station, D. J. Burdick (1♀, CAS). **Tuolumne:** Poopanaut Valley, Yosemite National Park, MEI (1♂, UCR). **Ventura:** Chuchupate Ranger Station (base of Frazier Mt.), PDH (1♀, CIS); Hungry Valley (5 mi S Gorman), PDH, C. W. O'Brien, G. I. Stage (2♀, 3♂, CAS; 5♀, 6♂, CIS). NEVADA: **Clark:** Juanita Spring Ranch (S Riverside), FDP and J. H. Parker (1♀, USU). **Douglas:** Spooners Lake, J. Slansky (1♂, CSDA). **Lyon:** 7 mi NE Wellington, MSW and J. S. Wasbauer (1♀, 1♂, CSDA). **Washoe:** Mt. Rose, RMB (2♂); Verdi, RMB, FDP (1♀, 2♂), MEI (1♂, UCR).

MEXICO: **Baja California Norte:** 1 mi S El Cóndor, JWB and DKF (1♂, SDNH); El Portezuelo (39 road mi S Catavina), WJP (3♂, CAS); 21 mi ESE El Rosario, WJP (1♂, CAS); Vallecitos area (Sierra San Pedro Mártir), JWB and DKF (1♀, SDNH), 29°22'N, 114°20'W, WJP (1♂, CAS).

Tachysphex musciventris Pulawski

(Figures 59, 60)

Tachysphex musciventris Pulawski, 1982:33, ♀, ♂. ! Holotype: ♀, California: San Diego Co., Borrego (UCD).

DIAGNOSIS.—The female of *musciventris* has a mesally sunken, densely pilose mesothoracic venter (Fig. 59b), unknown in

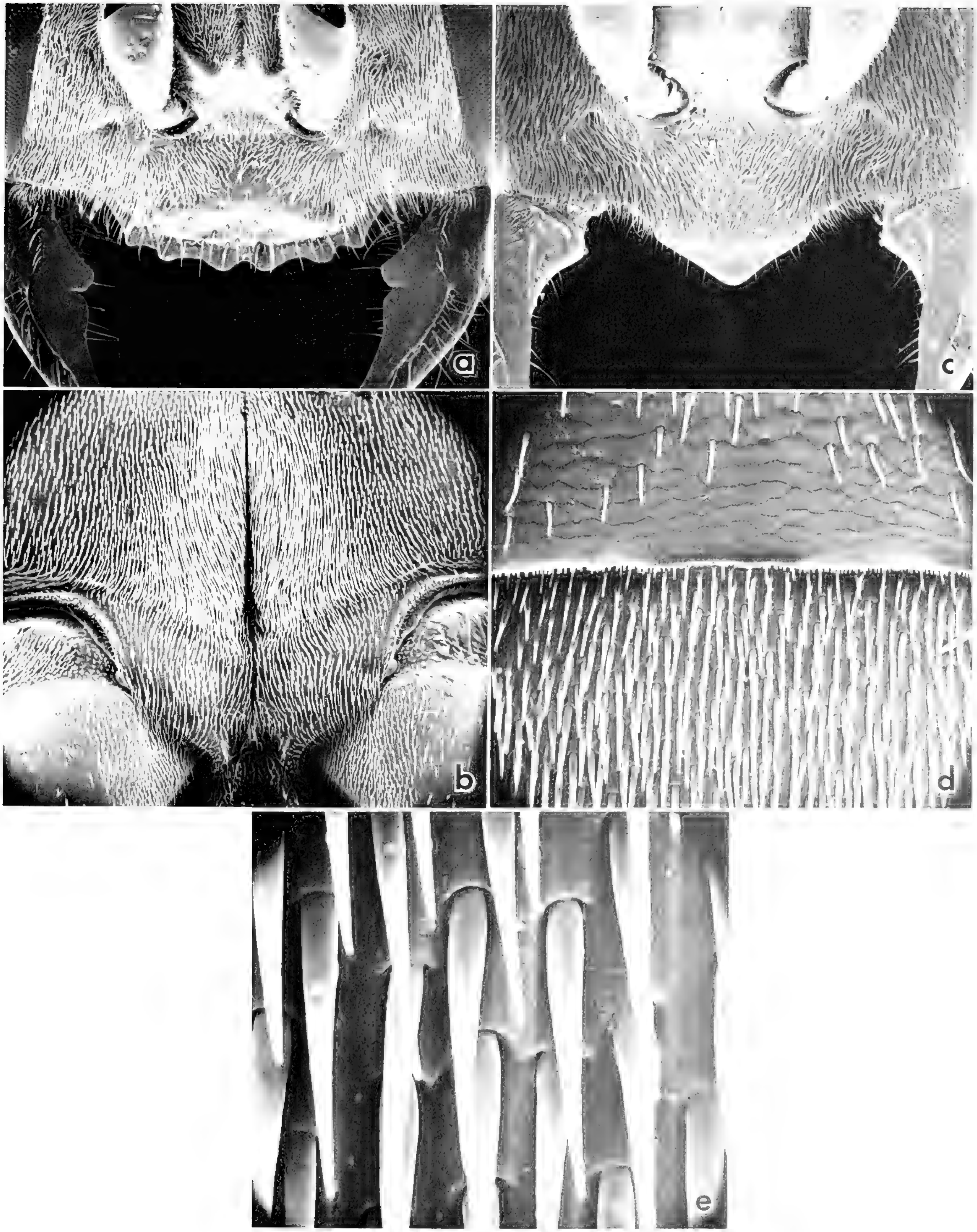

FIGURE 59. *Tachysphex musciventris* Pulawski: a—female clypeus; b—mesothoracic venter of female, c—male clypeus, d—sternal setae, e—same, higher magnification

FIGURE 60 Geographic distribution of *Tachysphex musciventris* Pulawski.

any other *Tachysphex*. Most specimens also have an undulate clypeal lip (Fig. 59a) and red hindlegs.

Males of *musciventris* and *tahoe* have a triangular clypeal lip (Fig. 57d, 59c), ill-defined mesopleural pnctures, and velvety pubescent sterna III–VI (integument all or largely concealed). Unlike *tahoe*, the vertex width in *musciventris* is 1.3–2.0× length (1.1–1.4 in *tahoe*), the hypoepimeral setae are appressed, and sternum II is velvety pubescent.

DESCRIPTION.—Frontal and scutal punctures nearly contiguous (a few punctures of scutal disk more than one diameter apart in some females). Vertex punctures even, less than one diameter apart, subcontiguous in many specimens. Mesopleuron dull, its punctures ill defined, shallow, contiguous or nearly so. Propodeal dorsum uniformly microareolate; side and hindface dull, strongly microsculptured, ridged (ridges evanescent in some specimens). Micropunctures of tergum II one to two diameters apart.

Setae appressed on mesothorax and femora; oriented posterolaterad on scutum at middle.

Head and thorax black. Terga I–V silvery fasciate apically (only laterally on female tergum V). Frontal vestiture silvery. Wings almost hyaline.

♀.—Clypeus (Fig. 59a): bevel equal to basomedian area or longer; lip in most specimens emarginate mesally, with one lateral incision on each side and with three pairs of obtuse projections, but in some individuals not emarginate and with admedian pair of projections only. Dorsal length of flagellomere I 2.2–2.8× apical width. Vertex width more than length. Mesothoracic venter sunken and densely pubescent along midline on posterior (horizontal) half (Fig. 59b). Tergum V with a few, scattered punctures. Pygidial plate shiny, punctate. Trochanteral venter shiny, sparsely punctate. Forefemoral venter with minute subcontiguous punctures that are somewhat sparse basally. Length 8.5–11.5 mm.

Integument not hidden by vestiture between antennal socket and orbit. Setae appressed on vertex, dense in mesosternal depression (as seen from in front forming a conspicuous patch).

Gaster red. Femora and tibiae all black in some specimens (females from Baja California Sur, CSDA; several females from El Rosarito and Mission San Borja areas, Baja California Norte, CAS; one from Monterey, California, UCD). In most specimens, fore- and midfemur black; foretibia red on inner face; midtibia black or red ventrally; hindfemur and hindtibia red. Tarsi red.

♂.—Mandibular inner margin not dentate (Fig. 59c). Clypeus (Fig. 59c): bevel equal to basomedian area or shorter; free margin not angulate between lobe and lateral section; lip roundly triangular, its corners obtuse, closer to each other than to orbits. Dorsal length of flagellomere I 1.3–1.7× apical width. Vertex width 1.3–2.0× length. Tergum VII in most specimens sparsely punctate basomedially. Sterna evenly, minutely punctate (punctures less than one diameter apart) except for narrow, apical stripe on sterna II–VI which is smooth, glabrous (Fig. 59d, e). Forefemoral notch pubescent. Foretarsus with rake or (some small individuals) foretarsomere with apical spine only; outer apical spine of foretarsomere II longer than tarsomere width, in most specimens longer than tarsomere III. Length 5.2–9.0 mm.

Vestiture partly obscuring sculpture between antennal socket and orbit. Vertex setae subappressed, sometimes erect (about 0.6 MOD long) on postocellar impression. Sternal pubescence velvety (Fig. 59d).

Gaster red or terga VI and VII and all sterna darkened. Legs black, tarsal apex reddish, sometimes also inner face of hindtibia.

LIFE HISTORY.—A single female from Mesa area, Arizona (UIM), was collected on flowers on *Baileya multiradiata* Harv. and Gray, and many males from Hungry Valley, California, were collected on flowers of *Euphorbia albomarginata* T. and G.

GEOGRAPHIC DISTRIBUTION (Fig. 60).—California to southwestern Texas, north to southwestern Utah, south to northwestern Mexico (including Baja California).

MATERIAL EXAMINED.—252♀, 258♂.

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** Dragoon Mts., Portal, 3 mi E Willcox. **Gila:** Globe. **Graham:** Roper Lake State Park. **Maricopa:** 8 mi S Buckeye, Gila Bend (also 18 mi S), 5 mi N Mesa, Rainbow Valley. **Mohave:** 8 mi E Mesquite (in Nevada), 16 mi N Wikieup. **Pima:** Silver Bell. **Pinal:** W Stanfield. **Santa Cruz:** 12 mi SW Patagonia, Tubac. **Yavapai:** 18 mi N Aguila. **Yuma:** Dateland, Ligurta, Parker, 15 and 22 mi N Yuma. CALIFORNIA: **Amador:** 5 mi E Jackson. **Fresno:** 10 mi W Coalinga. **Imperial:** Chocolate Mts. (Ogilby Road 3 mi S junction Hwy. 78), Fish Creek Mts., Glamis (also 3 mi N), Ocotillo, Palo Verde (also 3 and 8 mi S). **Inyo:** Wildrose Canyon. **Kern:** 14 mi N Blackwells Corner, Iron Canyon (El Paso Mts.), 19 mi W Shafter. **Lake:** Lucerne. **Lassen:** Bridge Creek Camp, Summit Camp (E Lassen Peak). **Los Angeles:** 1 mi S Acton, Littlerock, 2 mi S Pearblossom (also 12 mi NE), 2 mi NW Valyermo. **Modoc:** Cedar Pass. **Monterey:** Monterey, Seaside. **Riverside:** Anza, Boyd Desert Research Center (4 mi S Palm Desert), 18 mi W Blythe, 10 mi NW Cottonwood (Joshua Tree National Monument), Deep Canyon (3.5 mi S Palm Desert), 5 mi S Hemet, Highway 74 at Strawberry Creek, Indio, Keen Camp in San Jacinto Mts., Millard Canyon, 7 mi W North Palm Springs, Palm Canyon, Palm Desert, Palm Springs, Pinon Flat in San Jacinto Mts., Riverside (also 4 mi S), Shavers Summit, Strawberry Canyon, Thousand Palms, 10 mi E White Water. **San Bernardino:** 13 mi E Amboy, Baker (also 4 mi S), 3 mi W Barstow, 2 mi W Cajon Pass, Colton, 5 mi SE Hesperia, sand dunes 7 mi SW Kelso, Needles (also 11 mi N), 2 mi W Phelan, Red Mountain, 10 mi E Timico Acres, Vidal Junction. **San Diego:** Alpine, Borrego Valley, Boulevard–Manzanita, Coronado, Coyote Creek (Borrego Valley), 5 mi E Jacumba, Scissors Crossing. **San Luis Obispo:** 5 mi W Nipomo, 10 mi W Simmler. **Ventura:** Hungry Valley (5 mi S Gorman), Quatal Canyon (NW corner of county). NEVADA: **Clark:** 20 mi W Glendale, 5 mi N Searchlight. NEW MEXICO: **Dona Ana:** 4 and 11 mi N Las Cruces, Mesilla. TEXAS: **Hudspeth:** Sierra Blanca. UTAH: **Washington:** Santa Clara.

MEXICO: **Baja California Norte:** Cataviña (also 27 mi SE), 4 mi S El Cóndor, 4 mi NE El Rosarito (28°42′N, 113°58′W), 7 mi S Guadalupe, 25 km SE Laguna Chapala, 3 mi NE Mission San Borja, 6 mi E Ojos Negros, San Quintin, 6 mi NE Santa Rosalillita (28°45′N, 114°10′W), 1 mi E Santa Inés near Cataviña. **Baja California Sur:** 12 mi S Guillermo Prieto, 13 air km WNW La Purisima, 3.5 km WNW San Isidro, 5.8 mi S San Juanico, E edge of Sierra Placeres (27°35′N, 114°30′W). **Sonora:** 60 mi E San Luis, 23 km SW Sonoita.

Tachysphex occidentalis Pulawski

(Figures 61, 62)

Tachyspex occidentalis Pulawski, 1982:34, ♀, ♂. ! Holotype: ♂, California: Inyo Co.: 12 mi E Lone Pine (UCD).—Elliott and Kurczewski 1985: 293

DIAGNOSIS.—The female of *occidentalis* has a red hindfemur and hindtibia (all or partly), and the clypeal lip is evenly arcuate, not incised laterally (Fig. 61a). This combination is also found in *solaris*, most *apricus*, and rare individuals of other species. However, in *occidentalis* the humeral plate of the forewing base is partly dark, the mesopleuron is impunctate, the mesopleural vestiture does not conceal mesopleuron, and setae of the propodeal dorsum are oriented anterolaterad between the base and apex (in *solaris*, the humeral plate is uniformly ferrugineous, the mesopleuron is minutely punctate, the mesopleural vestiture largely conceals the integument, and most setae of the propodeal dorsum are oriented transversely; in *apricus*, the lateral setae are oriented posterad and join apicomesally). The following characters help separate *occidentalis* from occasional specimens of other species that have partly red legs and an entire clypeal lip. The scutal setae are oriented posterad, and sternum I is not depressed apically (in *texanus* and its relatives, the midscutal setae are oriented laterad, Fig. 90b and c, and sternum I has an apical depression, Fig. 91c and d). The clypeal lobe is relatively narrow, the distance between the lip corners being 1.5 × clypeal length or less (the clypeal lobe is broad in *antennatus* and *crassiformis*, and the distance between the clypeal lip corners is 1.7–2.5 × clypeal length). The axilla is evenly convex (axilla steplike or expanded in most *crassiformis*). The mesopleuron is finely sculptured (mesopleuron coarsely punctate to rugose in *irregularis*). Finally, the vertex setae are appressed posteriorly, and tergum II is fasciate apically (in *mirandus*, vertex setae are erect, and tergum II is asetose except laterally).

The male of *occidentalis* has an unusually narrow clypeal lobe (distance between lip corners about 0.6 of distance between lip and orbit), with the lip rounded laterally (Fig. 61b). In addition, the mandibular inner margin is not dentate or at most with a rudimentary tooth. The clypeus is equally narrow in *eldoradensis* and *hopi*, but the lip is angulate, and the mandibular inner margin has a well-defined tooth. Subsidiary recognition features of the male of *occidentalis* are: sternal punctures (Fig. 61c) about as large as those on the mesothoracic venter (markedly larger in some specimens); and the hypostomal carina expanded, broader than in most other species (but narrower than in most *lamellatus*).

DESCRIPTION.—Punctures subcontiguous on frons, scutum, mesothoracic venter, and trochanters. Vertex punctures no more than one diameter apart or (some specimens) a few interspaces larger than punctures. Mesopleuron dull, irregularly microsculptured, its punctures ill defined (especially in female). Propodeal dorsum and side microareolate, side microridged when seen from certain angles; hindface finely ridged. Discal micropunctures of tergum II one to two diameters apart. Sternum I with shallow apical depression. Hindcoxa not carinate.

Vestiture totally obscuring sculpture between antennal socket and orbit. Setae suberect on vertex (appressed posteriorly in female), about 1.0 MOD long; subappressed on scutal disk, oriented almost uniformly posterad; suberect on hypoepimeral area; appressed below mesopleural scrobe; appressed (female) or suberect, about 0.5 MOD long (male) on midfemoral venter apically. Setae of propodeal dorsum inclined obliquely anterad mesally, directed laterad laterally (lateral zone as wide as median zone or wider).

Head and thorax black; terga I–IV silvery fasciate apically, tergum V with rudimentary fascia. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 61a): middle section almost flat; bevel about as long as basomedian area; lip evenly arcuate, at most scarcely incised laterally; free margin shallower between lobe and orbit than in *antennatus* or *tarsatus*. Dorsal length of flagellomere I 2.0–2.6 × apical width. Vertex width 1.0–1.2 × length. Tergum V densely punctate or (some specimens) sparsely punctate mesally. Forecoxa with short, apicomedian process. Tarsomeres IV and V of most specimens slenderer than average in the *pompiliformis* group; hindtarsomere IV emarginate on about 0.65–0.75 of its length. Length 7–10 mm.

Gaster red or terga IV and V partly black. Fore- and midfemora black; fore- and midtibiae black or red; hindfemur red or largely black; hindtibia red or partly black; tarsi red or reddish.

♂.—Mandibular inner margin not dentate (Fig. 61b) or with evanescent tooth. Clypeus (Fig. 61b): bevel much shorter than basomedian area; free margin not angulate between lobe and

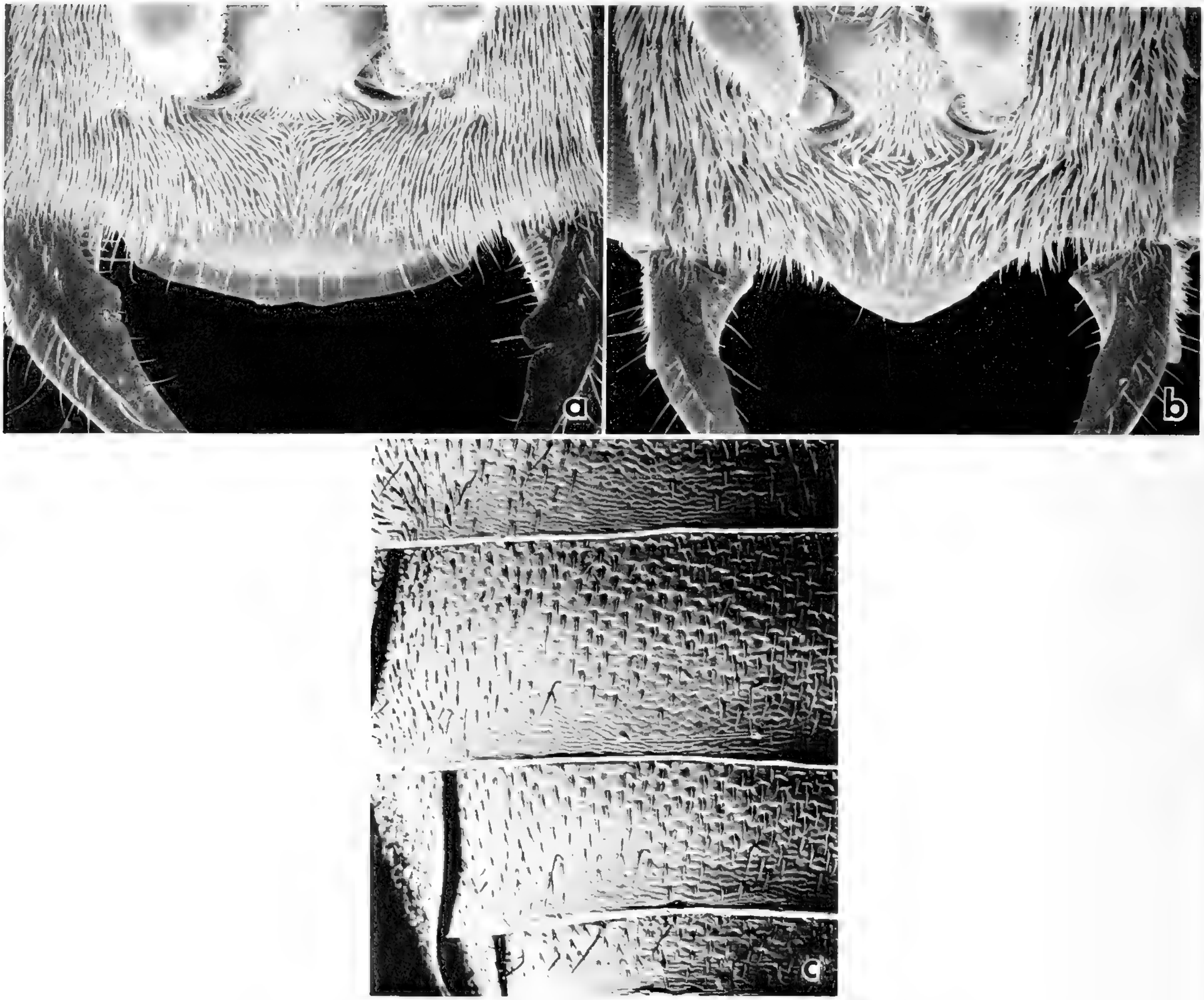

FIGURE 61 *Tachysphex occidentalis* Pulawski: a—female clypeus; b—male clypeus; c—male sterna.

lateral section; lobe arcuate, distance between its corners about 0.6–0.8 of distance between lobe and orbit. Dorsal length of flagellomere I 1.3–1.7× apical width. Vertex width 1.3–1.4× length. Sternal punctures as large as those on mesothoracic venter or larger, apical depression impunctate (Fig. 61c). Forefemoral notch shiny, glabrous. Forebasitarsus with none to four preapical rake spines; outer apical spine of foretarsomere II as long as foretarsomere III. Length 6–7 mm.

Gastral segments I–III or only terga I and II red, remainder black. Legs black, tibiae brown in some specimens; tarsal apex reddish.

LIFE HISTORY.—Elliott and Kurczewski (1985) report a nymph of the acridid *Schistocerca shoshone* (Thomas) as prey of *occidentalis*. A female from Wadsworth, Nevada (UCD), is pinned with two immature *Melanoplus*, probably *cinereus* Scudder (Acrididae), determined by D. C. F. Rentz.

GEOGRAPHIC DISTRIBUTION (Fig. 62).—Xeric areas west of the Rocky Mountains, north to Oregon and Idaho, south to New Mexico and Baja California (Norte).

MATERIAL EXAMINED.—116♀, 203♂ (ASU, CAS, CIS, CSDA, KWC, LACM, NYSU, OSDA, SDNH, UCD, UCR, UIM, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Apache:** Lukachukai. **Cochise:** 3 mi E Willcox. **Coconino:** 4.5 mi E Moenkopi. **Mohave:** Littlefield, 8 mi NE Mesquite (in Nevada). **Navajo:** Jadito Trade Post. CALIFORNIA: **Fresno:** Jacalitos Canyon. **Inyo:** Antelope Springs (15 mi S Big Pine), Deep Springs, Lone Pine (also 2 mi S, 3 mi N, 7.3 mi W, 12 mi NE), Owens Valley (sand dunes E Tinemaha), Saline Valley (NW end). **Kern:** 12 mi E Mojave, 14 mi W Shafter. **Lassen:** Hallelujah Junction. **Los Angeles:** 1 mi W Littlerock, 12 mi NE Pearblossom. **Mono:** 9 mi N Bishop, Chalfont, 7 mi SW Lee Vining, Mono Lake dunes. **Monterey:** Arroyo Seco Camp. **Plumas:** Chilcoot. **Riverside:** Anza. **San Bernardino:** Cronise Valley, Cronise Wash (15 mi E Baker), Four Corners, Kramer Hills, Twentynine Palms, Yermo. **San Diego:** Borrego Valley, Scissors Crossing. **San Luis Obispo:** 10 mi W Simmler. **Ventura:** Hungry Valley (5 mi S Gorman). IDAHO: **Cassia:** 2.5 mi S Malta. **Franklin:** Preston. **Fremont:** 6 mi NW St. Anthony, St. Anthony Sand Dunes. **Lincoln:** 4.5 mi E Dietrich, Shoshone. **Oneida:** 5 mi S Holbrook. NEVADA: **Churchill:** 12 mi NE Stillwater. **Clark:** Glendale. **Humboldt:** Orovada,

Winnemucca (also 10 mi N). **Lyon:** Fernley, Yerington. **Mineral:** Huntoon Valley sand dunes, Teels Marsh sand dunes. **Washoe:** Nixon, Patrick, 15 mi E Reno, Wadsworth (also 2.8 mi W). NEW MEXICO: **Dona Ana:** Mesilla. OREGON: **Harney:** 21.5 mi NW Fields sand dunes. UTAH: **Cache:** Logan (Dry Canyon). **Duchesne:** 5.5 mi W Roosevelt. **Emery:** Goblin Valley, N Goblin Valley (Buckskin Spring, Wild Horse Creek), NE Goblin Valley (4 air mi N Gilson Butte, 2 and 3.2 mi E Little Gilson Butte), San Rafael Desert (2.5 mi SW Iron Wash, 3 mi SSE Temple Mt., Woman Wash). **Grand:** Bartlett Flat (N Dead Horse Point). **Kane:** Coral Pink Sand Dunes. **Millard:** 6 and 15 mi N Delta, 12 mi NW Fillmore. **San Juan:** 25 mi S Moab. **Washington:** 11 mi N Saint George, Santa Clara. WYOMING: **Sweetwater:** 20 mi W Farson.

MEXICO: **Baja California Norte:** 4 mi NE El Rosarito (28°42′N, 113°58′W), Punta de Cabras (12 mi W Santo Tomás), San Quintín, 5 mi S Santa María, 1–3 mi SE Santa Rosalillita (28°44′N, 114°08′W).

Tachysphex solaris Pulawski

(Figures 63, 64)

Tachysphex solaris Pulawski, 1982:35, ♀, ♂. Holotype: ♀, California: San Diego Co.: Borrego Valley (UCD).

DIAGNOSIS.—*Tachysphex solaris* can be recognized by the color of the basal plates in the forewing: the humeral plate is uniformly yellowish (with a dark, median spot in some individuals), thus contrasting with the dark median plate. In other species the humeral plate is either all dark or yellowish anteriorly and dark posteriorly, thus not contrasting in color with the median plate or (some *ashmeadii*) contrasting only slightly. Subsidiary diagnostic features of *solaris* are: size small (body length 5.0–7.5 mm); clypeal free margin shallowly concave between lobe and orbit (Fig. 63a, b); mesopleural vestiture largely concealing integument; setae of propodeal dorsum oriented mainly transversely.

DESCRIPTION.—Clypeal free margin shallowly concave between lobe and orbit; bevel usually shorter than basomedian area but equal in some females; lip evenly arcuate, not emarginate mesally or incised laterally (Fig. 63a, b). Punctures fine, subcontiguous on frons, vertex, and mesopleuron; up to one or two diameters apart on scutum and mesothoracic venter; minute, sparse on mid- and hindtrochanteral venter. Propodeal dorsum microareolate, side microsculptured, hindface ridged. Discal micropunctures of tergum II about one diameter apart. Hindcoxa not carinate.

Vestiture totally concealing integument between antennal socket and orbit, largely so on mesopleuron and, in female, on fore- and midfemoral venter; setae appressed on vertex, scutum, femora, and beneath mesopleural scrobe, inclined on hypoepimeral area; midscutal setae oriented posterolaterad (transversely in some males); most setae oriented transversely on propodeal dorsum.

Head and thorax black, clypeal bevel yellowish brown in some specimens; mandible largely yellowish. Gastral terga I–IV silvery fasciate apically. Wings hyaline, humeral plate of forewing base uniformly yellowish in most specimens, but with dark spot in the single male from Glendale, Nevada (USU). Frontal pilosity silvery.

♀.—Clypeus (Fig. 63a): distance between lip corners 1.9–2.0× length. Dorsal length of flagellomere I 2.2–2.5× apical width. Vertex width mostly less than length, but more than length in some specimens. Length 5–7 mm.

Gaster red. Forefemur black, midfemur black or red, hindfemur red or basally black; tibiae red or fore- and midtibiae nearly all black; tarsi red.

FIGURE 62. Geographic distribution of *Tachysphex occidentalis* Pulawski

♂.—Mandibular inner margin with tooth. Clypeus (Fig. 63b): lip arcuate, distance between its corners about 1.6× clypeal length; corners ill defined, closer to orbits than to each other. Dorsal length of flagellomere I 1.6–2.0× apical width. Vertex

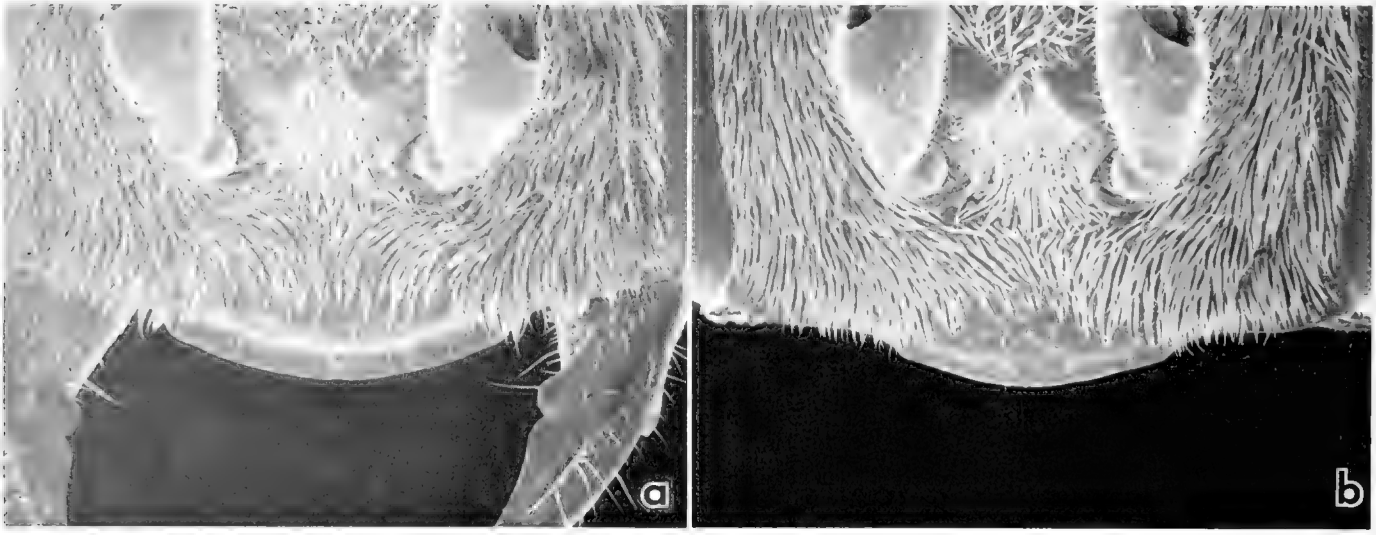

FIGURE 63. *Tachysphex solaris* Pulawski: a—female clypeus; b—male clypeus.

width 1.0–1.3× length. Sterna with minute, dense punctures, apical depression in many specimens contrastingly impunctate. Forefemoral notch pruinose. Forebasitarsus outer margin with none to four preapical spines that are up to two basitarsal widths long; apical spine of foretarsomere II longer than foretarsomere III. Length 5–6 mm.

Sternal vestiture dense, velvety in some specimens on sterna III and IV, apical depressions glabrous.

Gastral segments I–III red, remainder black. Femora black; tibiae black or reddish brown, hindtibia red in some specimens; tarsi red.

GEOGRAPHIC DISTRIBUTION (Fig. 64).—Central and southern California, southern Nevada, western and southern Arizona (xeric areas).

MATERIAL EXAMINED.—74♀, 32♂ (ASU, CAS, CIS, CSDA, MCZ, SDNH, TLG, UAT, UCD, UCR, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Maricopa:** Rainbow Valley. **Mohave:** 8 mi E Mesquite (in Nevada). **Pinal:** 5 mi NW Coolidge. **Yuma:** 10 mi W Aztec, 6 and 8 mi SE Parker, 15 mi E Yuma (also 18 mi NE). CALIFORNIA: **Imperial:** Glamis, Palo Verde, Pinto Wash. **Inyo:** Ballarat, 13 mi S Death Valley Junction, Lone Pine (also 2 mi E), S end Owens Lake, 15 mi S Panamint Springs. **Riverside:** 18 mi W Blythe, Hopkins Well, Thousand Palms. **San Bernardino:** Bagdad, 16 mi SW Baker on Basin road, 23 mi S Baker on Afton road, Colton Hills, Cottonwood Wash, Cronise Valley, Kelso (also 7 mi SW), Twentynine Palms (also 10 mi E). **San Diego:** Borrego Valley. NEVADA: **Clark:** Glendale (also 20 mi W).

Tachysphex apricus Pulawski

(Figures 65, 66)

Tachysphex apricus Pulawski, 1982:29, ♀, ♂. Holotype: ♂, California: San Diego Co.: Borrego Valley (UCD).—Elliott and Kurczewski 1985:293.

DIAGNOSIS.—*Tachysphex apricus* differs from all other species of the *pompiliformis* group by the orientation of setae on its propodeal dorsum (the median setae are inclined forward, but the lateral setae are directed obliquely backward and joining apicomesally) and also by the structure of the propodeal side (integument microsculptured but shiny, with fine, sparse punctures; Fig. 65b). Both characters are also found in species of the *brullii* subgroup, but the unspecialized apical tarsomere of the female of *apricus* is distinctive. In the male of *apricus*, sterna are simple (sterna III–V with graduli or a transverse sulcus in males of the *brullii* subgroup), and most individuals (Texan specimens are exceptional) can also be recognized by the compressed femoral notch whose glabrous bottom forms an obtuse, longitudinal crest (Fig. 65e). *Tachysphex idiotrichus* has a similar crest, but unlike that species the body vestiture is short in *apricus*.

DESCRIPTION.—Mesopleuron alutaceous, its punctures subcontiguous to (some females) about two diameters apart, inconspicuous (most specimens) to well defined. Propodeal dorsum dull, microareolate; side alutaceous, shiny, with minute, shallow punctures (Fig. 65b) that are mostly evanescent in male and absent in some specimens; hindface ridged. Tergum II with evanescent microsculpture. Sternum I shallowly depressed at apex. Hindcoxa carinate basally.

Vestiture totally obscuring sculpture between antennal socket and orbit, largely so on mesopleuron. Setae erect or suberect, 0.7–1.0 MOD long on vertex; appressed or subappressed on scutum (oriented posterad at middle); appressed or suberect (and then about 1.0 MOD long) on midfemoral venter. Median setae of propodeal dorsum (most setae in most specimens) inclined anterad, but lateral setae inclined obliquely posterad.

Head and thorax black. Gaster red or terga V–VII brown in some males; terga I–IV (I–IV in some males) silvery fasciate apically. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 65a): bevel about as long as basomedian area; lip arcuate, without median notch or lateral incisions. Dorsal length of flagellomere I 2.3–2.5× apical width. Frons shallowly punctate, most punctures less than one diameter apart. Vertex as wide as long or slightly wider, its punctures fine, about one diameter apart. Scutal punctures fine, one to two diameters apart, but many discal punctures often two to three diameters apart. Punctation of tergum V sparse to dense (see Geographic Variation below), apical depression impunctate. Pygidial plate (Fig. 65c) somewhat broader apically than in most species of the *pompiliformis* group. Fore- and midtrochanteral venter alutaceous, with minute, sparse punctures. Hindtarsomere IV dorsally emarginate on less than half length, insertion of hindtarsomere V close to base of emargination. Length 6.5–8.0 mm.

Legs partly red in most specimens, but all black in individuals from southern Texas and some individuals from southern Arizona (see Geographic Variation below for details).

♂.—Mandibular inner margin with small tooth (Fig. 65d). Clypeus (Fig. 65d): bevel shorter than basomedian area to nearly absent; lip arcuate, its corners obtuse, not prominent, closer to orbits than to each other. Dorsal length of flagellomere I 1.5–1.75× apical width. Frons dull, microreticulate. Vertex width 0.9–1.3× length; vertex punctures minute, about one diameter apart. Scutal punctures subcontiguous, but some discal punctures up to two diameters apart. Sterna very finely, very densely punctate and pubescent. Forefemoral notch variable (see Geographic Variation below). Foretarsus without rake; outer apical spine of foretarsomere II shorter than foretarsomere III. Length 5.5–6.0 mm.

Legs black, tarsal apex brownish.

Life History.—The only male examined from Hungry Valley, California (UCD) was collected on flowers of *Euphorbia albomarginata* T. and G.

As noted by Elliott and Kurczewski (1985), a female collected at Tucson, Arizona, is pinned with a phasmid, *Parabacillus hesperus* Hebard, more than four times its length. Phasmids are not known as prey of *Tachysphex*, and the record must be accepted with scepticism until new observations confirm or invalidate it.

Geographic Variation.—In most females tergum V is sparsely punctate, but it is densely punctate in a female from Sahuarita, Arizona and all 37 females studied from Kleberg County, southeastern Texas.

In most females the hindfemur, hindtibia, and hindtarsus are red, and the remaining legs are black (also hindcoxa, fore- and midtibia red in some specimens). The hindfemur is red, and the hindtibia and hindtarsus are largely red in specimens from San Luis Potosí area in Mexico (KU). The legs are all black (except tarsal apex reddish) in a female from Sahuarita, Arizona (UCD) and in the females from Kleberg County, Texas.

In most males, the distance between the clypeal lip corners is 1.1–1.2× clypeal length, but 1.3–1.4× in all 13 males examined from Kleberg County, Texas (the clypeal lobe is therefore longer).

In most males, the forefemoral notch is compressed, so that its glabrous bottom forms an obtuse, longitudinal crest (Fig. 65e). The notch's bottom is not compressed in the males from Kleberg County, Texas (CAS).

Geographic Distribution (Fig. 66).—Xeric areas between southeastern Texas, southern Utah, southern Nevada south to Mexico (Baja California, Zacatecas).

Material Examined.—76♀, 84♂ (ASU, CAS, CIS, CNC, CSDA, CSU, FSCA, HKT, KU, LACM, NYSU, OSU, TLG, UAT, UCD, UCR, USNM, USU).

Records.—UNITED STATES: ARIZONA: **Cochise:** 6 mi N Apache, Portal. **Coconino:** 4.5 mi E Moenkopi. **Maricopa:** 10 mi E Gila Bend, 3 mi SW Wickenburg. **Mohave:** 4 mi W Chloride, 8 mi E Mesquite (in Nevada), 15 mi SE Wikieup. **Pima:** 3 mi S Ajo, Organ Pipe Cactus National Monument, Sahuarita, Santa Rita Mts., Tucson. **Pinal:** W Stanfield. **Yavapai:** Bloody Basin, 10 mi NW Congress. CALIFORNIA: **Imperial:** Glamis, Palo Verde, Pinto Flat, Pinto Wash. **Inyo:** Antelope Springs, 2 and 5 mi E Big Pine, Big Pine Creek, Eureka Valley (12 mi N, 10 mi W Sand Dunes), Little Lake, 3 mi W Lone Pine, Tuttle Creek (2 mi SW Lone Pine). **Kern:** Kernville, Mojave. **Riverside:** 18 mi W Blythe, Magnesia Canyon, 3.5 and 4 mi S Palm Desert, San Andreas Canyon, San Timoteo Canyon, Shavers Summit. **San Bernardino:** 1 mi S Adelanto, Colton Hills, Cottonwood Wash, Granite Mts., 6 mi S Kelso, sand dunes 7 mi SW Kelso, Kramer, 3 mi S Kramer Junction, Lucerne Valley, Mitchell's Caverns, Providence Mts. State Park, 36 road mi E Twentynine Palms, Wheaton Springs, Yermo. **San Diego:** Borrego Valley, Mount Palomar, Scissors Crossing. **Ventura:** Hungry Valley (5 mi S Gorman), Sespe Canyon. NEVADA: **Clark:** Jean, Juanita Spring Ranch S Riverside, 20 mi S Searchlight. NEW MEXICO: **Dona Ana:** Las Cruces. **Otero:** Alamogordo, Alamo Canyon near Alamogordo. TEXAS: **Brewster:** Big Bend National Park (Nine Point Draw). **Kleberg:** 20 mi SE Kingsville ("Site 55"), Riviera Beach. **Ward:**

Figure 64. Geographic distribution of *Tachysphex solaris* Pulawski

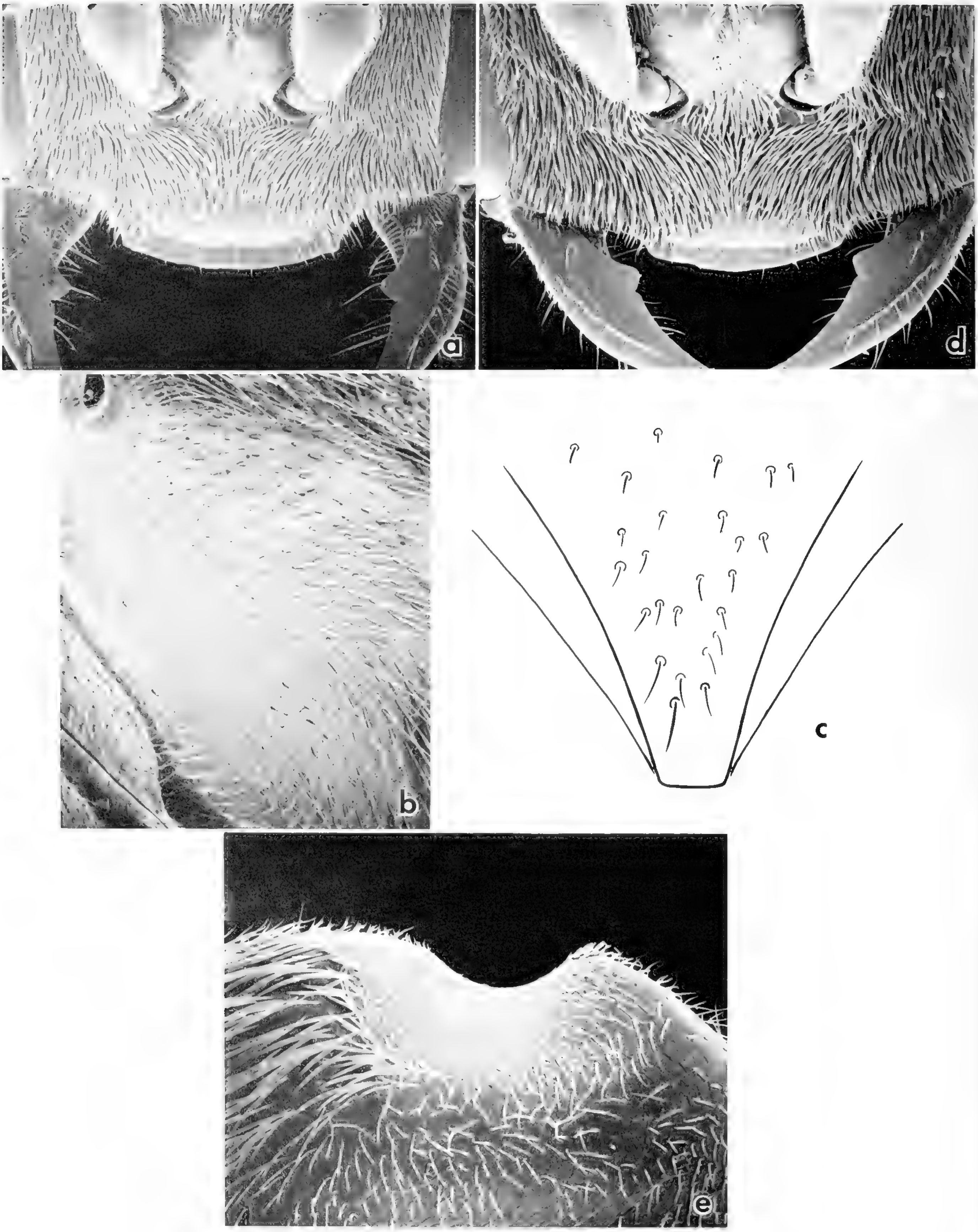

FIGURE 65 *Tachysphex apricus* Pulawski: a—female clypeus; b—propodeal side of female; c—pygidial plate of female; d—male clypeus; e—forefemoral notch of male

Monahans. UTAH: **Emery:** Buckskin Spring N Goblin Valley, 2 mi Little Gilson Butte (NE Goblin Valley). **Washington:** Gunlock, Leeds Canyon, Paradise Canyon.

MEXICO: **Baja California Norte:** San Angel 16 mi N Puertecitos. **Baja California Sur:** 35 km S Mulegé. **San Luis Potosí:** 29 mi SW San Luis Potosí. **Tamaulipas:** San Antonio (road 101 W Ciudad Victoria). **Zacatecas:** 9 mi N Ojocaliente.

FIGURE 66 Geographic distribution of *Tachysphex apricus* Pulawski

Tachysphex sulcatus sp. n.

(Figures 67, 68)

DERIVATION OF NAME.—Sulcatus is a Latin masculine adjective meaning furrowed; with reference to the mandibular sulcus.

DIAGNOSIS.—*Tachysphex sulcatus* has a dull, microsculptured mesopleuron. The shape of the clypeus and type of vestiture characterize the female: the clypeal lip is not incised laterally (Fig. 67a), the setae are appressed or nearly so on vertex, erect and 1.3 MOD long near hypostomal carina posteriorly, suberect on hypoepimeral area, and appressed below mesopleural scrobe. Several species are similar: *apricus* (which has a peculiar setal pattern on the propodeal dorsum), *miwok* (in which setae are appressed along the hypostomal carina), *occidentalis* (hindtibia all or partly red, while all black in *sulcatus*), and *tahoe* (clypeal lip weakly sinuate, while arcuate in *sulcatus*). Most females of *sulcatus* also have a longitudinal sulcus on the mandibular outer side, beyond the notch (Fig. 67c, d), but the sulcus is vestigial in some. It is vestigial or absent in other species.

In the male the clypeal lobe is rounded (free margin of lobe arcuate, not angulate laterally; Fig. 67e), as in *occidentalis* and *tipai*. In *sulcatus*, the clypeal lobe is broad (distance between lip corners about equal to distance between corner and orbit), the vertex width is about 1.1 × length, the setae are nearly erect on postocellar impression and nearly appressed on remaining vertex, the length of flagellomere II is about 2.0 × width, the mesopleural setae are appressed beneath scrobe, and sterna are finely punctate throughout. In *occidentalis*, the distance between lip corners is about 0.6–0.8 the distance between a corner and the orbit, sternal punctures are at least as large as those on the mesothoracic sternum, and the apical depressions of sterna II–V are impunctate. In *tipai*, the vertex width is about 1.4–1.6 × length, the vertex setae are erect, the length of flagellomere II is 2.25–2.5 × width, and the mesopleural setae are subappressed to suberect beneath scrobe.

DESCRIPTION.—Punctures less than one diameter apart on frons, vertex, scutum, and mesothoracic venter, about one diameter apart on vertex in some females. Mesopleuron dull, with ill-defined, contiguous punctures. Propodeal dorsum microareolate, side microareolate or microscopically ridged, hindface finely ridged. Sternum I without apical depression. Hindcoxa not carinate or weakly carinate basally.

Setae concealing integument between antennal socket and orbit; nearly erect on postocellar impression and nearly appressed on remaining vertex; almost uniformly oriented posterad on scutum; suberect on hypoepimeral area and appressed beneath scrobe; oriented anterolaterad on propodeal dorsum; appressed on midfemoral venter.

Head, thorax, and legs black, tarsal apex reddish. Gaster red or (one of the males studied) apical terga dark; terga I–III (I–IV in male) silvery fasciate apically. Frontal vestiture silvery. Wings almost hyaline.

♀.—Clypeus (Fig. 67a, b): bevel longer than basomedian area, with several sparse, unusually large punctures; lip arcuate, not incised laterally, mesally not marginate or with a rudimentary notch; free margin shallowly concave between lobe and orbit. Mandibular outer side sulcate beyond notch (Fig. 67c, d). Dorsal length of flagellomere I 2.2–2.4 × apical width. Vertex width

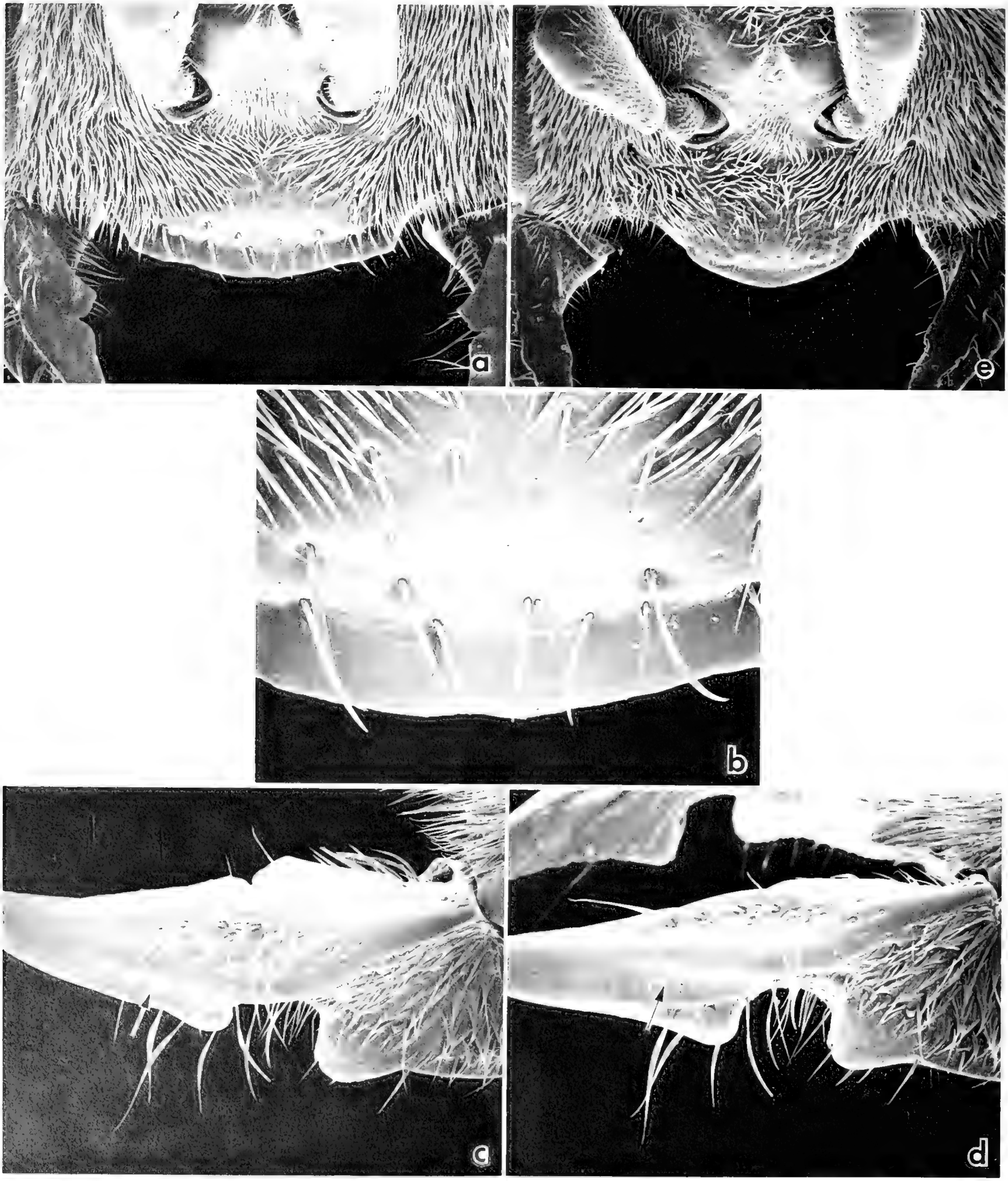

Figure 67. *Tachysphex sulcatus* sp. n. a—female clypeus, b—anteromedian portion of female clypeus, c—female mandible (arrow indicates the sulcus), d—same, different orientation, e—male clypeus.

0.9–1.1 × length. Discal micropunctures of tergum II about two to three diameters apart. Tergum V sparsely punctate mesally, apical depression impunctate. Pygidial plate alutaceous, sparsely punctate. Femora and trochanters densely uniformly punctate. Length 8–9 mm.

♂.—Mandibular inner margin not dentate (Fig. 67e). Clypeus (Fig. 67e): bevel about as long as basomedian area, with several punctures that average larger than in other species; clypeal free margin shallowly concave between lobe and orbit, not angulate between lobe and lateral section (free margin of lobe rounded); lip corner vestigial, separated by a distance that is about equal to clypeal length and also to distance that separates corner from orbit. Dorsal length of flagellomere I 1.5–1.75 apical width. Vertex width 1.1 × length. Sterna densely punctate throughout. Forefemoral notch pruinose. Forebasitarsus without preapical rake spines or (some specimens) with one subbasal spine. Outer apical spine of foretarsomere II no longer than tarsomere width. Length 6 mm.

Geographic Distribution (Fig. 68).—Northern California to Baja California Sur, adjacent areas of Nevada.

Collecting Period.—22–23 April (Baja California), 9 June to 22 October (U.S.A.).

Material Examined.—Holotype: ♀, California: Los Angeles Co.: Angeles Crest Highway, Arroyo Seco, Switzer Station, 29 July 1977, PHA (CAS, Type #15908).

Paratypes (31♀, 9♂): UNITED STATES: CALIFORNIA: **Contra Costa:** Mt. Diablo, 2,000 ft, 11 July, year not indicated, FXW's handwriting (1♀, CAS). **Inyo:** Antelope Springs, 1 July 1961, J. S. Buckett (1♀, UCD). **Lassen:** Doyle, 30 Aug 1978, TRH (1♀, CSDA). **Los Angeles:** Kenter Canyon (NW Los Angeles), 29 Aug 1978, C. D. Nagano (1♀, LACM); Lake Hughes, EIS, 1 Aug 1958 (1♀, UCD); Tanbark Flat, 20 and 21 June 1956, RCB (2♀, UCD), 21 June 1956, RCB (1♂, CAS), 23 June 1956, RMB (1♀, UCD), 8 July 1950, FXW (1♀, 2♂, CAS), 10 July 1956, RMB (1♀, CAS), 14 July 1956, RMB (1♂, UCD), 18 July 1956, RMB (1♀, UCD); Vasquez Rocks in San Gabriel Mts., 17 July 1964, R. R. Snelling (1♀, LACM). **Mono:** 11 mi N Bridgeport, 7 July 1961, PMM (1♀, CAS), RMB (1♀, 1♂, UCD); Tom's Place, 2,195 m, 4–5 July 1967, PMH (1♂, CAS); 1 mi S Tom's Place, 8 Aug 1962, LAS (1♂, UCD). **Riverside:** Bautista Canyon 11 mi SE Hemet, 9 June 1974, KWC (1♀, CAS); San Timoteo Canyon, 14 Sep 1972, MSW and A Hardy (2♀, CAS; 1♀, CSDA). **San Bernardino:** Cajon, 17 July 1956, H. R. Moffitt (1♀, UCD); Cleghorn Campground (14 mi N San Bernardino), 27 Sep 1975, D. Burnett (1♀, CSDA); Mid Hills, TLG, 16 June 1980 (1♀, TLG), 19–27 June 1980 (1♂, TLG); Mountain Home, 12 Sep 1953, EIS (1♀, UCD); San Bernardino Mts. 12 mi S Mentone, 11 July 1956, RCB (1♀, UCD); Thurman Flats Picnic Area, 22 Oct 1965, PHA (1♀, CAS); Wildwood Canyon 3 mi E Yucaipa, 15 June 1976, TLG (1♀, TLG). **San Diego:** Culp Canyon in Anza Borrego State Park, 12 June 1958, EIS (1♀, UCD); Mount Laguna, 5 July 1963, JAP (1♂, CIS); Pine Valley, 6 Aug 1977, Lee Guidry (1♀, SDNH). **Santa Barbara:** Santa Ynez Mts., 24 June 1959, PMM (1♀, UCD). **Santa Clara:** San Antonio Valley (3.5 mi N Del Puerto Canyon road), 21 Aug 1962, JAP (1♀, CIS). NEVADA: **Douglas:** Minden, RMB (1♀, UCD).

MEXICO: **Baja California Sur:** 4 mi WSW Miraflores, MSW, 23–24 April 1979 (1♀, CAS).

Figure 68. Geographic distribution of *Tachysphex sulcatus* sp. n.

Tachysphex tipai sp. n.

(Figures 69, 70)

Derivation of Name.—Named after the Tipai Indians (also called Kimia) of southern California, where the holotype was collected; noun in apposition.

Diagnosis.—The female of *tipai* has: vertex setae erect; mesothoracic venter sparsely punctate on each side of midline; fore- and midfemora basoventrally without micropunctation but with a few, sparse punctures (Fig. 69d); flagellomeres II–X longer than in most other *Tachysphex* (Fig. 69b) (for example, length of flagellomere II 3.5–4.0 × width). These characters are shared

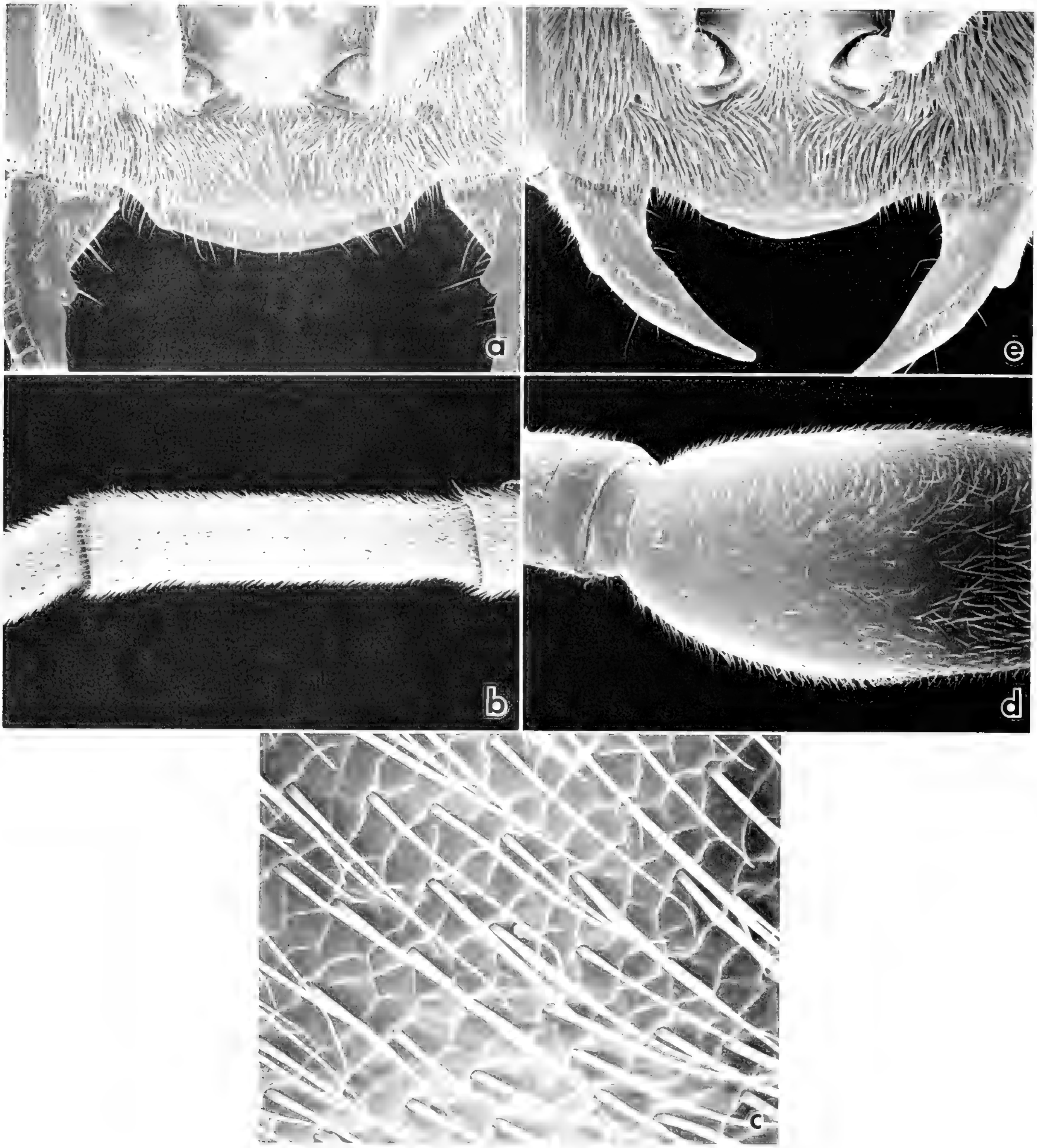

FIGURE 69. *Tachysphex tipai* sp. n.: a—female clypeus, b—female flagellomere II, c—sculpture of female mesopleuron; d—base of female forefemur; e—male clypeus.

with *mirandus*, but in the latter the basal plate of sternum II is broad apically, and the body length is 8.0–12.0 mm. In *tipai*, the basal plate is angulate (acutely or nearly so), and the body length is 6.5–8.0 mm. Furthermore, in many *mirandus* punctures of the lateral clypeal section are larger than those on the adjacent frons (punctures of equal size in *tipai*).

The male of *tipai* has erect vertex setae, the clypeal lobe is indistinctly delimited laterally (Fig. 69e), the inner mandibular

margin is not dentate (Fig. 69e), and the mesopleuron is dull, impunctate, or with ill-defined punctures. In most specimens punctures of the mesothoracic venter are many diameters apart on both sides of midline (but no more than one diameter apart in some). The long flagellomere II (length 2.25–2.5× width) is a subsidiary diagnostic feature. *Tachysphex mirandus* is similar, but its sterna II–IV are sparsely punctate, and the clypeal lip is triangular, whereas in *tipai* sterna II–IV are densely punctate, and the clypeal lip is obtusely angulate to arcuate.

Another recognition feature of *tipai* is the orientation of setae on the propodeal dorsum. In most specimens, all median setae are inclined anterad along the midline, though in some individuals a few basomedian setae are inclined posterad. In most other species of the *pompiliformis* group, many of the basomedian setae are inclined posterad.

Two or three undescribed species are similar to *tipai*. The setae on their propodeal dorsum are conspicuous, mainly parallel to each other, nearly appressed in dorsal view and form an angle of less than 45° with the integument in lateral view, and the male clypeal lobe is well defined, angulate laterally. In *tipai*, the setae on the propodeal dorsum are suberect in dorsal view and form an angle of more than 45° with the body surface in lateral view.

Description.—Clypeal free margin less concave between lobe and orbit than in *antennatus, tarsatus,* or *semirufus*. Punctures nearly contiguous on frons, one to two diameters apart on vertex, many diameters apart on mesothoracic venter (but less than one diameter along midline). Mesopleuron evenly microsculptured, impunctate below scrobe (Fig. 69c) or (some males) with shallow, ill-defined punctures. In most specimens mesothoracic venter sparsely punctate (except densely punctate along midline), but punctures no more than one diameter apart in a male from Alamos, Mexico (CAS). Propodeal dorsum and side microareolate, side of some individuals with vestigial microridges when seen from certain angles; hindface ridged. Hindcoxa not carinate.

Vestiture not entirely concealing integument between antennal socket and orbit. Setae erect on vertex, about 1.0 MOD long; oriented posterolaterad on scutum at middle; inclined on mesopleuron; on propodeal dorsum forming an angle wider than 45° with integument in lateral view, oriented anterad along midline, or (some specimens) a few basomedian setae oriented posterad; appressed or nearly so on midfemoral venter.

Head and thorax black. Gaster red (female, some males) or (most males) base of tergum I and terga IV–VII or V–VII brown or black; gaster all black in a male from Alamos, Mexico. Legs black in most specimens, with tarsal apex brown, but hindtibia red apicoventrally in some females from Borrego Valley, all tibia red in single female from Andreas Canyon, California, and legs largely red in single female from El Golfo, Mexico (red are: midtibia largely, hindfemur, hindtibia, and all tarsi). Frontal vestiture silvery. Gastral terga I–IV (female) or I–V (male) silvery fasciate apically. Wings hyaline or slightly infumate.

♀.—Clypeus (Fig. 69a): bevel longer than basomedian area, lip evenly arcuate, not emarginate mesally or incised laterally. Dorsal length of flagellomere I (Fig. 69b) and II 2.75–3.25 and 3.5–4.0× apical width, respectively. Vertex width 1.1–1.3× length. Punctures of scutal disk up to two diameters apart. Discal micropunctures of tergum II several diameters apart. Tergum V with a few, sparse punctures, apical depression impunctate. Mid- and hindtrochanteral venter shiny, impunctate. Fore- and midfemora basoventrally without micropunctures, but with a few, sparse punctures (Fig. 69d) that are evanescent in some individuals. Length 6.5–8.0 mm.

♂.—Inner mandibular margin not dentate (Fig. 69e). Clypeus (Fig. 69e): bevel shorter than basomedian area, lip evenly arcuate or obtusely angulate, its lateral corner not prominent (clypeal free margin not or scarcely angulate on each side of lobe); distance between corners equal to 1.1–1.3 of clypeal length, equal to 0.9–1.1 of distance between corner and orbit. Dorsal length of flagellomere I 1.7–2.2× apical width; length of flagellomere II 2.25–2.5× width. Vertex width 1.4–1.6× length. Punctures of scutal disk almost contiguous. Sterna evenly punctate from base to hindmargin or punctures evanescent on apical depression of sterna II–V; punctures finer than those of mesothoracic venter. Forefemoral notch covered with microscopic, suberect setae. Forebasitarsus without preapical rake spines; outer apical spine of foretarsomere II equal to tarsomere width or shorter. Length 4.8–5.8 mm.

Sternal pubescence not velvety.

Life History.—Unlike most species of the *pompiliformis* group, *tipai* is a katydid collector. Two females examined are pinned with young katydid nymphs, both Decticinae, determined by D. C. F. Rentz. One female is from Borrego Valley, California (UCD), and the prey is *Ateloplus notatus* Scudder. The other is from Kingsville, Texas (TAI), and the prey is *Pediodectes* sp. Some specimens from Apple Valley, California, were collected on flowers of *Euphorbia albomarginata* T. and G., and the single female from Sierra Juárez, Baja California Norte was collected on *Hyptis emoryi* Torr.

Geographic Distribution (Fig. 70).—California, Arizona, Utah, southern Texas, and northern Mexico (Sonora, Baja California), mainly sandy areas including deserts.

Collecting Period.—24 February (Alamos, Sonora) to 28 May (Vacaville area, California).

Material Examined.—Holotype: ♀, California: Riverside Co 18 mi W Blythe, 23 March 1983, WJP (CAS, Type #15028)

Paratypes: 88♀, 48♂ (specimens for which depository is not indicated are all in UCD): UNITED STATES: ARIZONA: **Cochise:** 14 mi W Tombstone, RMB (1♂) FDP (2♂, CAS, UCD). **Maricopa:** 18 mi S Gila Bend, S. A. Gorodenski, J. M Davidson, M. A. Cazier (1♀); 3 mi SW Wickenburg, P. Torchio and GEB (1♀, USU). **Pima:** Organ Pipe Cactus National Monument, G. L. Jensen and W. J Turner (1♂, WSU); Santa Catalina Mts., F. W. Werner, J. C. Bequaert, H. Elton M. Nurein: Sabino Canyon (1♀, UAT) and Molino Basin (1♀, UAT). **Santa Cruz:** Nogales, Ex R. C. L. Perkins collection (4♀, including one with missing gaster, BMNH). **Yavapai:** 8 mi N Aguila, FDP (1♀, USU). **Yuma:** Quartzsite: 4 mi S JWMS (1♀, CIS); 7 mi S, WJP (1♀, CAS); 14 mi S, R. O. Schuster (1♀). 32 mi S DSH (2♀), D. R. Miller (1♀). CALIFORNIA: **Alameda:** Arroyo del Valle, W. J Turner (1♀, CIS). **Amador:** Pioneer, O. W. Richards (1♀, 1♂, BMNH); Volcano, MEI (1♀). **Colusa:** 21 mi SW Williams, D. R. Miller (1♀). **El Dorado:** Kyburz, S C. Kuba (1♀, CAS). **Fresno:** 12 mi W Coalinga, JWMS (1♂). **Imperial:** S end of Chocolate Mts. (Ogilby road 3 mi S junction with Highway 78), MSW and J Slansky (1♀, 1♂, CSDA); 2 mi NW Glamis, JAP (1♂, CIS); Ogilby road 6 mi N junction with Yuma–San Diego road, MSW and J. S. Wasbauer (1♀, CAS; 1♀, 1♂, CSDA); 3 mi S Palo Verde, C. A. Toschi (1♀, CIS). **Inyo:** Death Valley (Wildrose Canyon), R. M. Brown (1♀, CAS); Deep Springs, MSW and J. S. Wasbauer (1♂, CSDA); Surprise Canyon (Panamint Mts.), JAP (1♀), Townes Pass, F. G. Andrews (1♀, CSDA). **Kern:** Dove Spring Canyon (¾ mi N Ricardo, W Highway 6), C. A Toschi (1♀, CIS); Dove Well, P. Rude (1♂, CIS); Short Canyon (6 mi W Inyokern), JWMS (1♀, 2♂, CIS); 2 mi W Woffard Heights, C. A. Toschi (1♀, CIS). **Mendocino:** North California Coastal Range Preserve, 5 mi N Branscomb, REC (1♂, CIS) **Mono:** Paradise Camp, ASM (1♀). **Riverside:** Andreas Canyon, RMB (1♀), 18 mi W Blythe, DSH (1♀), MEI (1♀), WJP (1♀, CAS), Pinon Flat, FXW (1♂, CAS). San **Bernardino:** Apple Valley, PDH (2♀, 1♂); 5 mi W Essex, D. R. Miller (2♀); Granite Pass, J. C. Hall (1♀, USNM); 12 mi SE Ivanpah, B. J. Adelson (3♀), PDH (1♂)

FIGURE 70. Geographic distribution of *Tachysphex tipai* sp. n.

Kramer Hills, E. C. Hall (1♂, CAS, 2♂, 1♀, UCD). Kramer Junction, EIS (1♂). Mid Hills, TLG (1♂, TLG). 1 mi S Mojave River Forks in San Bernardino Mts., E. Fisher (1♀, CSDA). upper Morongo Valley, R. B. Roberts (1♂, OSU). Pipes Canyon (6 mi W Pioneertown), TLG (1♂, CAS). Providence Mts., TLG (1♂, CAS, 4♂, TLG). Sacaton Springs (New York Mts.), TLG (1♂, CAS). Twentynine Palms, KWC (1♀, CAS). Yucca Valley, KWC (1♀, CAS). **San Diego:** Borrego State Park (Coyote Canyon), MEI (1♂, UCR); Borrego Valley, RMB (1♀, CAS; 3♀, UCD); near Buckman Springs, FXW (1♂, CAS); Torrey Pines State Park, R. B. Parks (1♀, SDNH). **Solano:** Cold Creek (11 mi N Vacaville), G. C. Eickwort (1♀, CU). **Stanislaus:** Del Puerto Canyon (Frank Raines Park), PHA (1♀, CAS). **Trinity:** Hayfork, J. A. Chemsak (1♀, CIS); Hayfork Ranger Station, JAP (1♀, CIS). **Tulare:** Ash Mountain (Kaweah Power Station), D. J. Burdick (1♀, CAS). **Ventura:** Hungry Valley (5 mi S Gorman), PDH (5♂, CAS; 7♂, CIS), C. W. O'Brien (1♀, CIS). NEVADA: **Clark:** Saint Thomas Gap (ca. 15 mi SE Overton), R. C. Bechtel and J. B. Knight (1♀, NSDA). TEXAS: **Culberson:** 26 km N Van Horn, TLG (1♀, CAS). **Hidalgo:** McAllen Botanical Garden, C. C. Porter (1♂, FSCA). **Kimble:** Junction, WJP (2♀, 2♂, CAS). **Kleberg:** Kingsville, Jim Johnson (1♀, TAI). **Presidio:** 3 mi E Presidio, HEE (1♀, MCZ). **Upton:** Rankin, Michener and Beamer (2♂, KU). UTAH: **Garfield:** Calf Creek, TLG (1♀, UCD).

MEXICO: **Baja California Norte:** Cataviña, WJP (1♀, CAS); Diablito Canyon (E face of Sierra San Pedro Mártir), JAP (1♀, CIS); 19 mi E Ojos Negros, JWB and DKF (1♀, SDNH); San Felipe (1♂, CAS); 40 mi S San Quintín, WJP (1♂, CAS); Sierra Juárez, P. A. Opler (1♀, CIS). **Baja California Sur:** 22 mi ESE Bahía Tortugas, WJP (1♂, CAS); El Pescadero (Playa Los Cerritos), MSW and J. Slansky (2♂, CAS, CSDA); Los Barriles, MSW (1♀, CSDA); Punta Abrejos road 15 mi W San Ignacio, MSW (2♀, CSDA); 11 mi NE San Isidro, N. Bloomfield and DKF (1♀, SDNH); E edge of Sierra Placeres (27°35'N, 114°30'W), WJP (1♂, CAS). **Sonora:** Alamos, PHA (4♀, 4♂, CAS); 6 mi N El Golfo, MSW (1♀, CSDA).

Tachysphex mirandus Pulawski

(Figures 71, 72)

Tachysphex mirandus Pulawski, 1982:32, ♀, ♂. ! Holotype: ♀, California: San Bernardino Co.: Palm Springs (USNM).

DIAGNOSIS.—Terga I–IV are asetose (except somewhat pubescent laterally) in females of *mirandus*, some females of *semirufus*, and some females of *tipai*. In other species terga II–IV are finely setose throughout, though the setae may be partly worn off in old specimens. Unlike *semirufus*, the fore- and midfemoral venter of *mirandus* is not uniformly micropunctate, but has several sparse punctures with alutaceous interspaces (Fig. 71b). Unlike *tipai*, the basal platform of sternum II is broad apically in *mirandus* (acutely angulate or nearly so in *tipai*).

The male of *mirandus* can be recognized by the mesally nonpubescent, largely glossy, and sparsely punctate sterna II–VI, combined with the nondentate mandibular inner margin, triangular clypeal lip (Fig. 71c), and the clypeal free margin not angular between the lip and the lateral section.

Subsidiary recognition features of both sexes are: punctures larger on lateral clypeal section than on adjacent frons (the difference is slight in some specimens); mesopleural setae erect or nearly so (almost as in *semirufus*); horizontal part of mesothoracic venter in most specimens glossy and sparsely punctate (as in most *tipai*), contrasting with the dull, strongly microsculptured mesopleuron.

DESCRIPTION.—Frons below midocellus punctatorugose to sparsely punctate. Punctures one or two to many diameters apart on vertex and scutum (except subcontiguous near scutal margins); several diameters apart (but one diameter in some females) on horizontal portion of mesothoracic venter; mainly several diameters apart on trochanteral venter. Vertex alutaceous, concave in most specimens. Mesopleuron dull, microareolate to coarsely microsculptured, with shallow, inconspicuous punctures that are about one diameter apart on prepectus. Horizontal part of mesothoracic venter (except in specimens with dense punctation) and trochanteral venter shiny, alutaceous. Propodeal dorsum microareolate; side microareolate, also microridged in most specimens; hindface ridged or (some specimens) ridges evanescent. Hindcoxa not carinate. Midfemur (also fe-

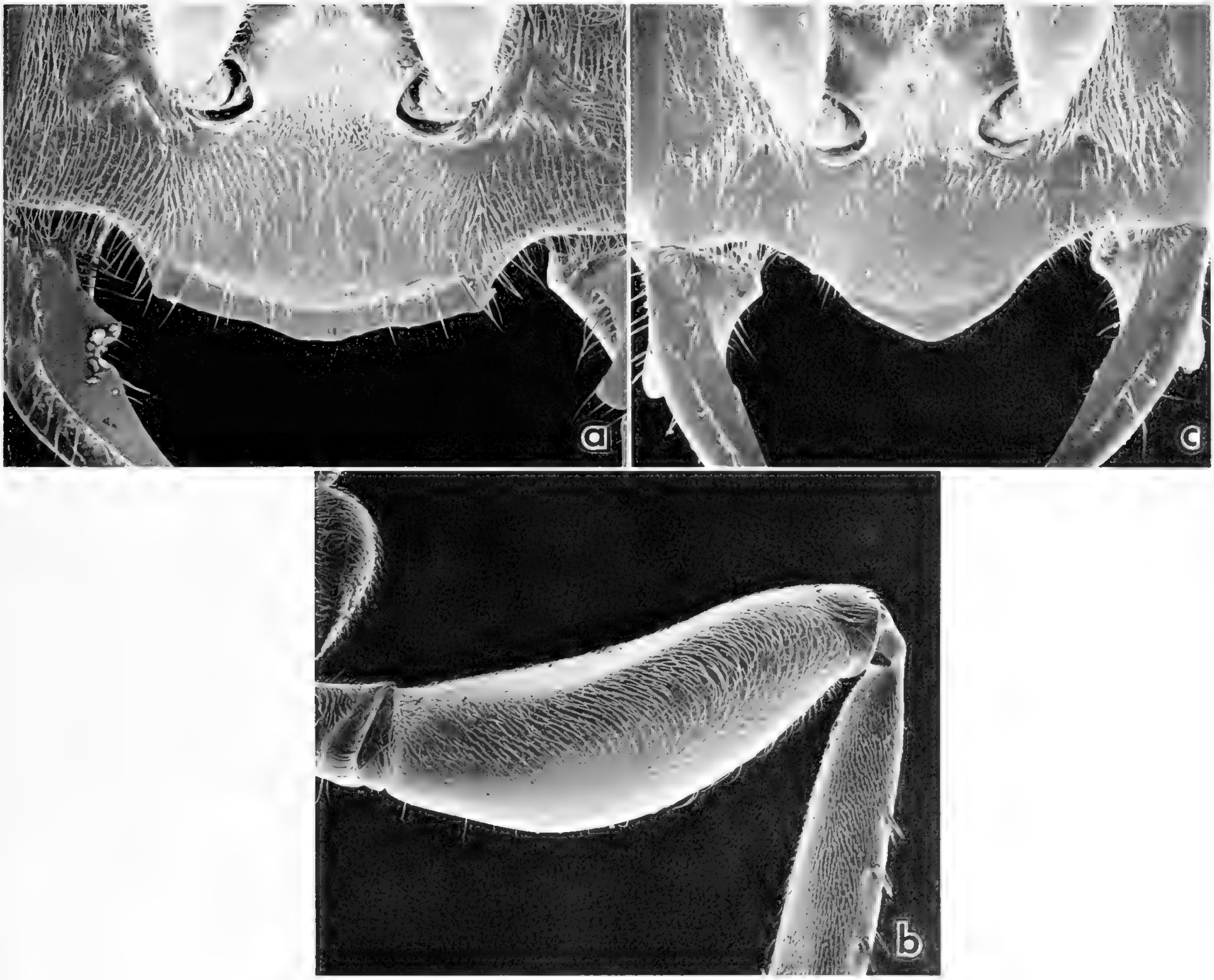

FIGURE 71. *Tachysphex mirandus* Pulawski: a—female clypeus; b—female midfemur; c—male clypeus.

male forefemur) basoventrally alutaceous or unsculptured, with a few, sparse punctures (Fig. 71b).

Setae erect, 1.0 MOD long on vertex; suberect to appressed on scutum, 0.6 MOD long anterolaterally, longitudinally to transversely oriented at middle; 1.0 MOD long on mesopleuron; suberect on distal half of midfemoral venter, 0.5–0.6 MOD long in female, about 1.0 MOD long in male. Most setae of propodeal dorsum inclined anterad (almost erect in some specimens).

Head and thorax black, gaster red. Fore- and midfemur black, female hindfemur black or red, male hindfemur partly red. Fore- and midtibia black, hindtibia red or (some females) black. Tarsi black or (males, some females) midtarsal apex and hindtarsus red. Terga not fasciate. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 71a): bevel longer than basomedian area; lip sinuate, obtusely produced mesally, not incised laterally. Dorsal length of flagellomere I 2.6–3.0× apical width. Vertex width 1.0–1.1× length in most specimens (vertex concave), but 1.6× length in a female from Panoche, California (vertex flat). Terga II–V alutaceous, glabrous except somewhat pubescent laterally. Length 8–12 mm.

♂.—Mandibular inner margin not dentate (Fig. 71c). Clypeus (Fig. 71c): free margin not angulate or scarcely angulate between lip and lateral section; lip triangular; bevel about as long as basomedian area. Dorsal length of flagellomere I 2.0–2.2× apical width. Vertex width 1.3–1.5× length. Terga with minute punctures that are several diameters apart on tergum II, interspaces alutaceous or unsculptured; most punctures of tergum VII more than one diameter apart. Sterna II–VI not pubescent (except laterally), glossy, sparsely punctate (except dull, densely microsculptured basally sterna II–V). Forefemoral notch shiny, glabrous. Forebasitarsus with four preapical rake spines; outer apical spine of foretarsomere II longer than foretarsomere III. Length 8.5–9.0 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 72).—Xeric areas of Arizona, Nevada, southern California, and Baja California.

COLLECTING PERIOD.—Markedly earlier than for most other

FIGURE 72. Geographic distribution of *Tachysphex mirandus* Pulawski.

species: 20 January to 14 April; a very worn specimen was collected near Pioneertown, California on 5 May.

MATERIAL EXAMINED.—31♀, 7♂ (CAS, CIS, CSDA, UCD, UIM, USNM, WJP).

RECORDS.—UNITED STATES: ARIZONA: **Mohave:** 4 mi S Hoover Dam. CALIFORNIA: **Fresno:** Pinoche (28 Mar). **Imperial:** 9 mi W Coyote Wells (26 Mar), Ocotillo (22 Mar), Yuha Desert (15 Feb). **Inyo:** S end of Owens Valley (25 Mar). **Kern:** 3 mi NW Indian Wells (12 Apr), Short Canyon 7 mi NW Inyokern (15 Mar) and 6.5 mi N Inyokern (12 Apr), 7 mi E Walker Pass (25 Apr). **Los Angeles:** Little Rock (22 and 28 Mar). **Riverside:** Palm Springs (11 Feb), Whitewater (14 Apr). **San Benito:** Panoche (29 Mar). **San Bernardino:** 5 mi S Essex (26 Mar), Needles (5 Mar), 14 mi E Newberry (31 Mar), 7 mi NW Pioneertown (5 May), Trona (4 Apr). **San Diego:** Borrego Valley (2 and 11 Apr), Borrego Springs (30 Mar). **San Luis Obispo:** Cuyama Valley 30 mi W Maricopa (21 Mar). **Tulare:** Kaweah Power House (20 Jan). NEVADA: **Nye:** Johnnie (28 Mar), 16 mi E Lathrop Wells (1 Apr), Mercury (28 Mar, 24 Apr).

MEXICO: **Baja California Norte:** 21 mi ESE El Rosario (17 Mar); Sierra Juárez: Upper Cantillas Canyon (19 Mar), E face of Sierra San Pedro Mártir: Diablo Canyon (6 Apr). **Baja California Sur:** 16 mi E Rosarito (26 Mar).

Tachysphex verticalis Pulawski

(Figures 73, 74)

Tachysphex verticalis Pulawski, 1982:36, ♀, ♂. ! Holotype: ♀, California: Riverside Co.: 9 mi W Beaumont (UCD).

DIAGNOSIS.—*Tachysphex verticalis* differs from other species of the *pompiliformis* group in having a uniformly areolate mesopleuron (Fig. 73b) and propodeal side, and constrastingly ridged propodeal hindface. In addition, the longer than wide vertex (slightly wider than long in some females) is distinctive, as is the markedly convex middle section of the clypeus. In the female, the clypeal lip has two lateral incisions (Fig. 73a), as in *crenulatus* and *glabrior*; the vertex has a shiny, median sulcus that extends posterad from the postocellar impression; and the pygidial plate is broad apically (Fig. 73c). In the male, sterna III–VI have well-developed graduli (as in *glabrior, idiotrichus,* and *irregularis*). Because of the narrow vertex and microareolate thorax side, *verticalis* may be confused with species of the *brullii* subgroup. However, the female tarsomere V is simple (apicoventral margin not expanded into a lobe, claws short, not prehensile). In the male, setae of the propodeal dorsum oriented anterad from the base to apex combined with the impunctate mesopleuron are distinctive.

DESCRIPTION.—Vertex with shiny, longitudinal sulcus that emerges from postocellar impression. Mesopleuron and propodeum dull, impunctate, uniformly microareolate (Fig. 73b) except propodeal hindface ridged, somewhat shiny. Hindcoxa carinate, carina expanded basally.

Scutal setae appressed, at middle oriented posterad; a few scattered setae suberect, about 0.7 MOD long.

Head, thorax, and legs black, tarsal apex brownish (reddish in many specimens), gaster red, with black, basal spot, darkened apically in some males. Terga I–III (I–IV in male) silvery fasciate apically. Wings almost hyaline.

♀.—Clypeus (Fig. 73a): bevel longer than basomedian area; lip weakly arcuate, with two lateral incisions on each side, in some specimens with rudimentary, mesal notch. Dorsal length of flagellomere I 2.0–2.4 × apical width. Frons dull, microsculptured, punctate, most punctures on upper half about one diameter apart. Vertex width 0.9–1.1 × length. Vertex punctures in most specimens subcontiguous mesally, many diameters apart near orbit and (some individuals) on whole surface. Scutum microsculptured, evenly punctate, discal punctures about one diameter apart. Tergum V with a few, scattered punctures, its apical depression impunctate. Pygidial plate shiny, its punctures dense to (some individuals) sparse, its apex broader than average in the *pompiliformis* group (Fig. 73c). Forefemoral venter impunctate, microsculptured, somewhat shiny. Length 8–10 mm.

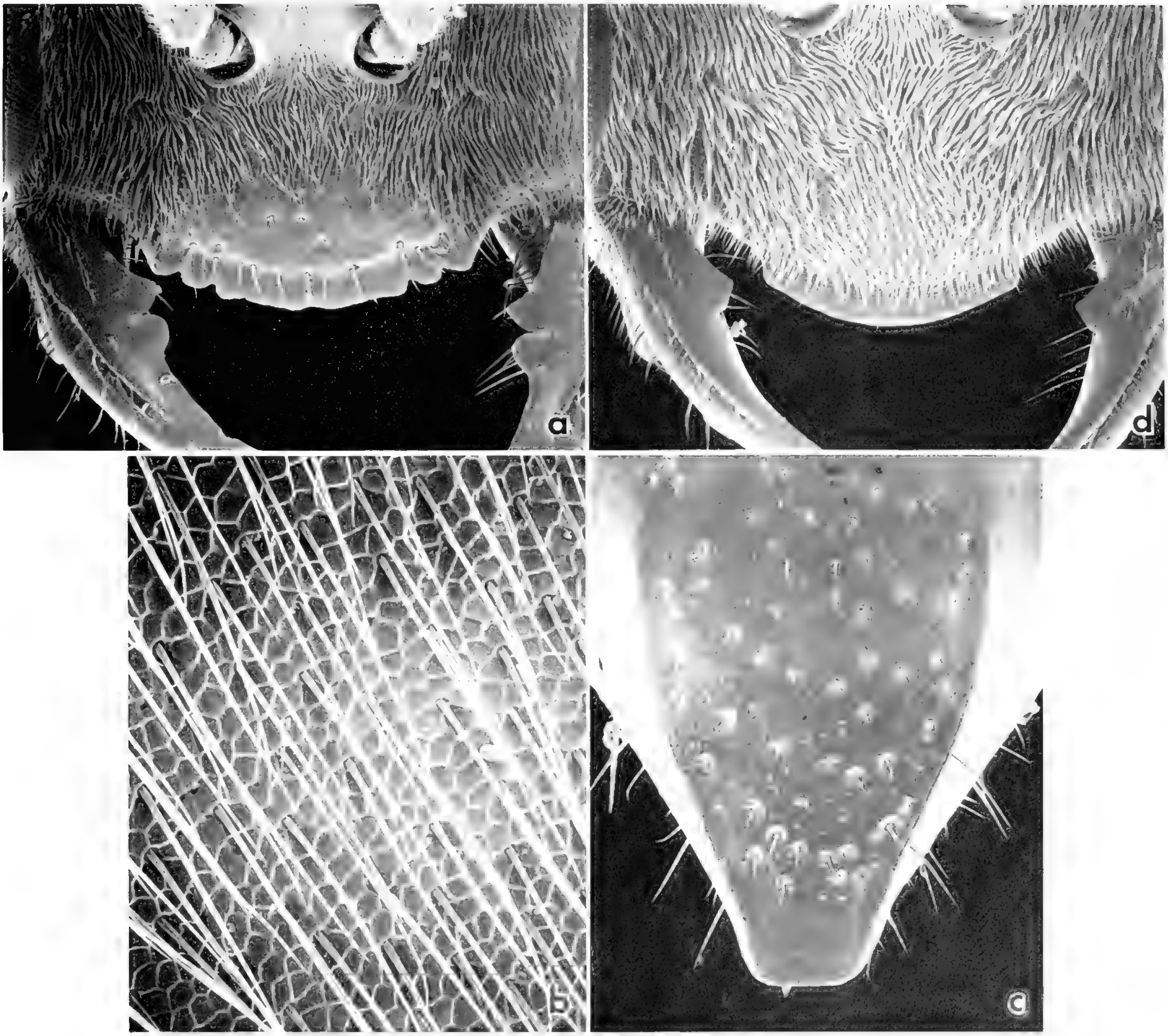

FIGURE 73. *Tachysphex verticalis* Pulawski: a—female clypeus, b—mesopleural sculpture of female, c—pygidial plate of female; d—male clypeus

Setae erect, 1.0–1.3 MOD long on vertex; 1.7–2.0 MOD long on lower gena; appressed or erect, slightly less than MOD, on midfemoral venter.

♂.—Mandibular inner margin with tooth (Fig. 73d). Clypeus (Fig. 73d): bevel dull, indistinct, or absent; lip evenly arcuate, its lateral corners obtuse, closer to orbit than to each other. Dorsal length of flagellomere I 1.3–1.6× apical width. Frons dull, microsculptured, shallowly, indistinctly punctate, punctures almost contiguous. Vertex microsculptured, punctate, punctures less than one diameter apart anteriorly and mesally, at least one diameter apart near orbit behind postocellar impression; vertex width 0.7–0.9× length. Scutal punctures even, subcontiguous. Terga densely microsculptured, but some discal micropunctures of tergum II two to three diameters apart. Sterna finely, densely punctate throughout, sterna III–VI with graduli. Forefemoral notch pruinose. Foretarsus without rake; outer apical spine of foretarsomere II much shorter than foretarsomere III. Length 5.5–9.0 mm.

Setae erect, 1.1–1.3 MOD long on vertex; 1.4–1.6 MOD long on lower gena. Femoral vestiture appressed.

Frontal vestiture golden above or with golden tinge, rarely silvery.

LIFE HISTORY.—A male from Meyer Canyon, California (CSDA) was collected on flowers of *Eriogonum fasciculatum* Benth.

GEOGRAPHIC DISTRIBUTION (Fig. 74).—Northern Mexico, California and adjacent areas of northern Nevada, Arizona and Utah; also isolated in Idaho.

MATERIAL EXAMINED.—116♀, 208♂.

RECORDS.—UNITED STATES: ARIZONA: Cochise: Bisbee, Box Canyon (Chi-

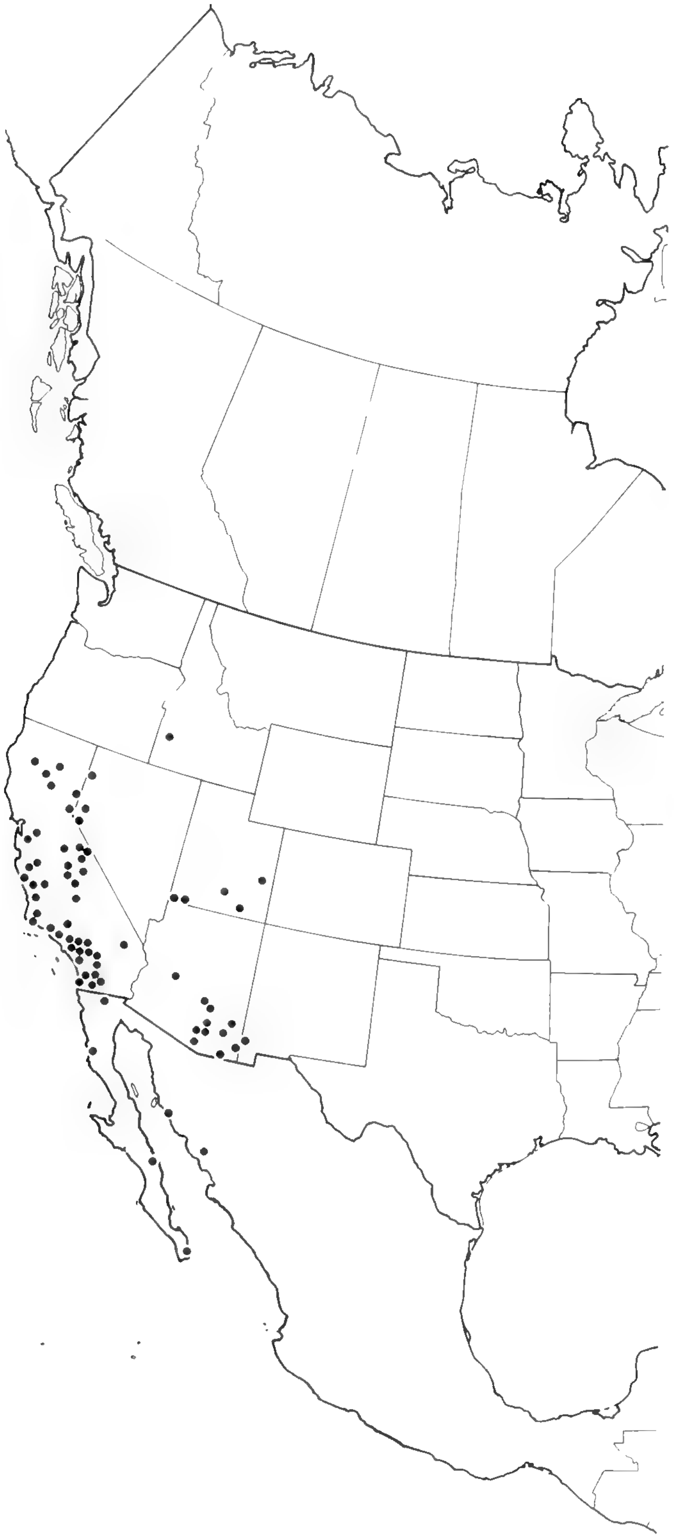

FIGURE 74. Geographic distribution of *Tachysphex verticalis* Pulawski.

ricahua Mts.), Portal, Skeleton Canyon (6 mi SE Apache), 2 mi E Willcox. **Gila:** Gila River 3 mi SW Christmas. **Graham:** Roper Lake State Park. **Pima:** Baboquivari Mts., Gates Pass, 2 mi E Robles Pass, Sabino Canyon, Tanque Verde, Tucson. **Pinal:** Boyce Thompson Arboretum (3 mi W Superior). **Yavapai:** Congress. CALIFORNIA: **Alameda:** Tesla Road. **Butte:** 1 mi NE Pulga. **Fresno:** Barton Flat, 13 mi W Cedar Grove, Hume Lake, Warthan Canyon. **Inyo:** Antelope Springs (8 mi SW Deep Springs), 3 mi W Big Pine, Big Pine Creek, 10 mi N Bishop, Lone Pine Creek, Symmes Creek, Westgard Pass (also 4 mi W). **Kern:** 2 mi W Frazier Park, Kernville. **Lassen:** Hallelujah Junction. **Los Angeles:** Camp Baldy, Charlton Flat (San Gabriel Mts.), Claremont, Crystal Lake Road, Elizabeth Canyon, Gorman, La Crescenta, Little Eaton Canyon, Mt. Wilson Road, Monrovia, Sangus, Santa Susana Pass, Tanbark Flat in San Gabriel Mts. **Mariposa:** Jerseydale (12–14 mi NE Mariposa). **Monterey:** Mill Creek (Santa Lucia Mts.), Paraiso Springs, 4 mi S San Ardo, 4 mi W Soledad. **Orange:** Hot Springs Canyon, Upper Trabuco Canyon. **Placer:** Lake Tahoe. **Riverside:** Anza, Banning, 9 mi W Beaumont, Park near Idyllwild, Pinyon Flat, Riverside, San Timoteo Canyon, Whitewater. **San Benito:** New Idria Road 4 mi SW junction Panoche Road. **San Bernardino:** Cajon, Cajon Junction, Hole-in-the-Wall (Providence Mts.), Meyer Canyon Road (5 mi NW Devore), Mill Creek Canyon, Oak Glen, Upper Santa Ana River, Wildwood Canyon, 3 mi SE Yucaipa. **San Diego:** Julian, Laguna Mts. road, La Jolla, Lake Henshaw, Little Cedar Canyon, Point Loma, Poway, Rose Canyon, San Diego (Mission Gorge), Scissors Crossing, Sorrento, Torrey Pines State Park, Warner Springs (also 9 mi S). **San Luis Obispo:** Creston, Nacimiento Dam, 3 mi NW Paso Robles. **Santa Barbara:** Bluff Camp (San Rafael Mts.), 3 mi W Cachuma Lake, Davey Brown Campground (12 mi NE Los Olivos), Los Prietos, Santa Ynez Mts., Surprise Stone. **Santa Clara:** San Antonio Valley (3.5 mi N Del Puerto Canyon road). **Shasta:** Hot Creek Post Office, Redding. **Stanislaus:** Del Puerto Canyon. **Trinity:** Junction City, 3 mi W Weaverville. **Tulare:** Ash Mountain (Kaweah Power Station), Three Rivers. **Ventura:** Foster Park, Sespe Canyon, Wagon Road No. 2 Campground (18 air mi WSW Gorman). IDAHO: **Owyhee:** 2 mi SW Murphy. NEVADA: **Douglas:** 3 mi S Genoa, Minden. **Storey:** Geiger Summit. **Washoe:** 54 mi NW Gerlach. NEW MEXICO: **Hidalgo:** Granite Gap (18 mi N Rodeo). UTAH: **Garfield:** Bullfrog Creek area near Lake Powell, Calf Creek, Escalante River. **Grand:** Moab. **Washington:** Leeds Canyon, Paradise Canyon, Snow Canyon.

MEXICO: **Baja California Norte:** 10 mi E Bahia San Quintin, 4 mi S La Rumorosa, San Quintín. **Baja California Sur:** 4 mi WSW Miraflores, 17 mi S Mulegé. **Sonora:** Cócorit, 6 km NNW San Carlos.

Tachysphex opata sp. n.

(Figures 75, 76)

DERIVATION OF NAME.—Opata is a Pima Indian word meaning "hostile people," "enemies," and referring to an Indian tribe that lived in northwestern Mexico and southeastern Arizona (where the holotype was collected); noun in apposition.

DIAGNOSIS.—*Tachysphex opata* has a finely, evenly punctate mesopleuron combined with a nonridged propodeal side (microridged in many females) and an apically nondepressed sternum I. A subsidiary recognition feature is the glabrous anterior portion of the propodeal side (along the metapleuron). Sternum II is distinctive in most females: the hindmargin of its basal plate is biemarginate (Fig. 75b), although the emarginations are ill defined (Fig. 75c) or absent in some specimens. Occasional females of *pinal* also have a biemarginate basal plate. Most *opata* have radially oriented midscutal setae that form a rosettelike pattern (as in *ashmeadii*, some *crassiformis*, and some *yolo*), but in some individuals the midline setae are oriented contrastingly posterad, as in *texanus* and its relatives. Unlike *ashmeadii*, the male of *opata* lacks graduli, and its clypeal free margin is deeply concave between lobe and orbit; furthermore, the labrum is nearly flat in *opata* but is markedly convex in most *ashmeadii* (both sexes). In *texanus* and its relatives, sternum I has an apical depression and the propodeal side is ridged (except some *yolo* and some *yuma*). Unlike *opata, crassiformis* has an unusually broad clypeal lobe and a distinctive axilla (see that species for details).

DESCRIPTION.—Middle clypeal section markedly convex. Labrum slightly convex near free margin. Punctures less than one diameter apart on frons, vertex, and scutum, or (some females) midscutal punctures several diameters apart; punctures fine, even, subcontiguous on mesopleuron and mesothoracic venter.

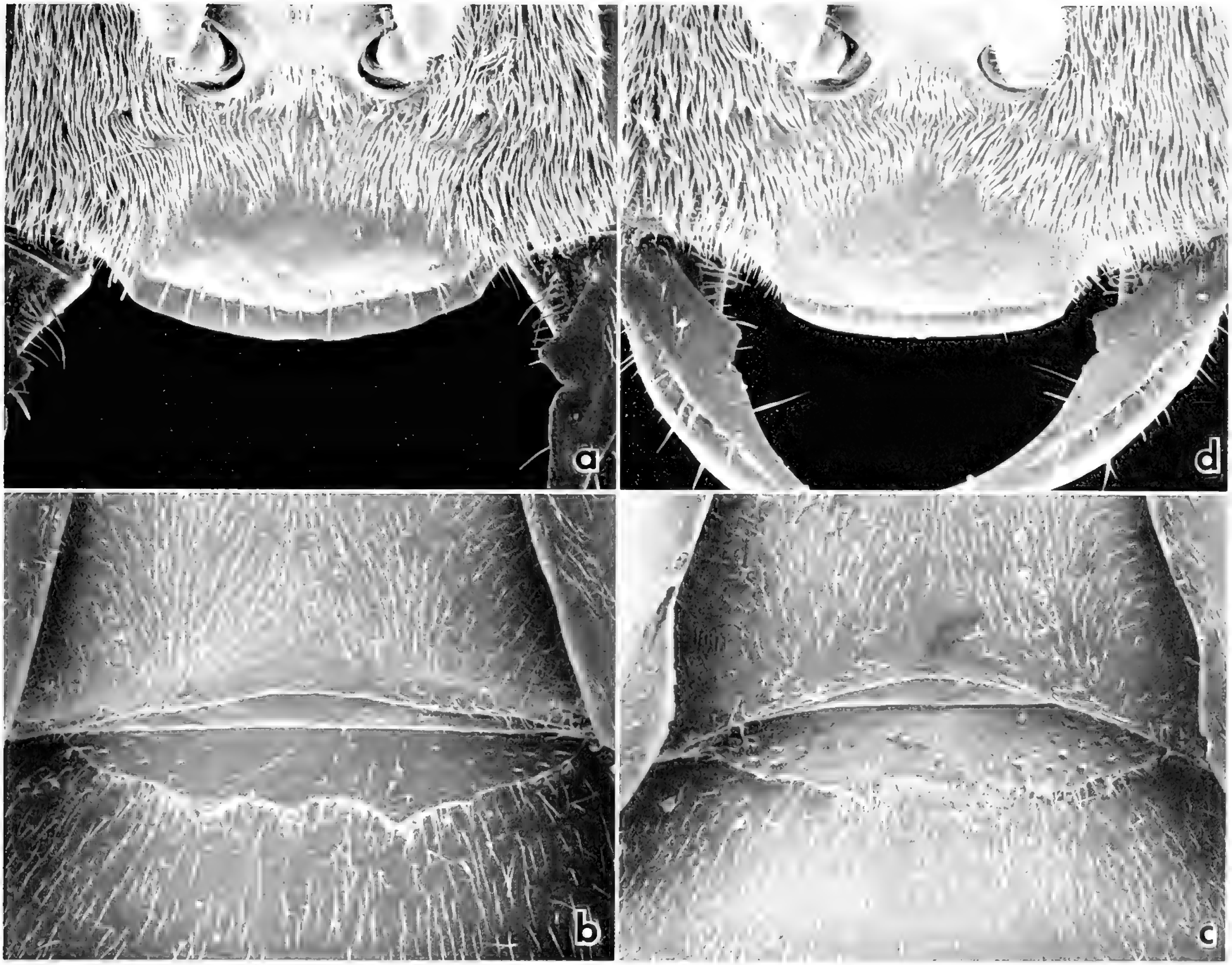

FIGURE 75. *Tachysphex opata* sp. n.: a—female clypeus; b—female sterna I and II; c—same of another specimen, d—male clypeus.

Propodeal dorsum evenly microareolate, hindface ridged. Sternum I without apical depression.

Integument between antennal socket and orbit totally hidden by vestiture as seen from most angles. Setae nearly erect, about 0.7–0.9 MOD long on vertex; inclined on mesopleuron; appressed or nearly so on midfemoral venter; inclined, diverging obliquely anterad on propodeal dorsum; midscutal setae forming rosettelike pattern (all setae of the rosette oriented radially in most specimens, but midline setae oriented posterad in a female from La Mesa, California, one from Coyotes area, Mexico, and one from San Quintín, Baja California Norte). Propodeal side glabrous along metapleuron.

Head, thorax, and legs black, tarsal apex reddish. Gaster red or (males from Baja California Sur) gastral segment I or segments I–II black. Frontal vestiture silvery. Terga I–IV fasciate apically (fascia of tergum IV interrupted). Wings almost hyaline.

♀.—Clypeus (Fig. 75a): bevel longer than basomedian area; lip arcuate, not emarginate mesally, concave (but not really incised) laterally. Dorsal length of flagellomere I 2.0–2.2 × apical width. Vertex width 0.9–1.3 × length. Propodeal side microscopically ridged or (some specimens) microareolate and finely punctate (except impunctate anteriorly). Tergum V sparsely punctate, impunctate on apical depression. Pygidial plate shiny, sparsely punctate. Sternum II setose except glabrous apically; its basal platform in most specimens with biemarginate hindmargin (Fig. 75b, c): with two emarginations that are separated by median projection (emarginations and projection of varying shape, rudimentary or absent in some specimens). Trochanteral venter closely micropunctate. Length 7–10 mm.

♂.—Mandibular inner margin with tooth (Fig. 75d). Clypeus (Fig. 75d): bevel about as long mesally as basomedian area; lip evenly arcuate to nearly straight, separated from bevel by well-defined sulcus; lip corners well defined, separated by distance that equals about 1.2 of clypeal length; clypeal free margin markedly more concave between lobe and orbit than in *ashmeadii*. Dorsal length of flagellomere I 1.6–1.7 × apical width. Vertex width 1.0–1.1 (Baja California Sur) or 1.3–1.5 × (Portal, Arizona) length. Propodeal side microareolate and punctate (except impunctate anteriorly). Sterna evenly, microscopically punctate. Forefemoral notch pruinose. Forebasitarsus without preapical

FIGURE 76. Geographic distribution of *Tachysphex opata* sp. n.

rake spines; outer apical spine of foretarsomere II shorter than tarsomere width. Length 7–8 mm.

LIFE HISTORY.—The females from Schurz area, Nevada, were collected on flowers of *Eriogonum inflatum* Torr. and Frém.

GEOGRAPHIC DISTRIBUTION (Fig. 76).—Southeastern Arizona, southwestern Texas, Nevada, southern California, and Mexico (including Baja California).

COLLECTING PERIOD.—30 April to 19 June (U.S.A.), 24 May to 4 Aug (Mexico).

MATERIAL EXAMINED.—Holotype: ♂, Arizona: Cochise Co.: Portal, 27 May 1983, Veronica Ahrens (CAS, Type #15905).

Paratypes (37♀, 14♂): UNITED STATES: ARIZONA: **Cochise:** Portal, same data as holotype (2♂, CAS), 18–19 Apr, WJP (2♂, CAS); 2 mi E Texas Canyon, 11 May, A. D. Telford (2 ♂, UCD); Tombstone, 15 June, E. C. Van Dyke (1♀, CAS), 30 May, E. L. Klee (8♀, 1♂, CAS). **Gila:** Roosevelt Lake, 11 May, H. and M. Townes (1♀, UCD). **Graham:** Roper Lake State Park, 25 May, WJP (1♀, CAS). **Santa Cruz:** Atascosa Mts., 22 May, G. D. Butler (1♀, UCD); Canelo, 27 May, A. and H. Dietrich (1♂, CU); Nogales, 30 Apr, RMB (1♀, UCD); Tumacacori Mts., Bear Grass Tank, 30 May, Olson (1♀, UAT). CALIFORNIA: **Inyo:** Lone Pine Creek, 6 June, RMB (1♀, UCD). **San Diego:** La Mesa, 19 June, FXW (1♀, CAS); Scissors Crossing–Valle San Felipe, 4 May, R. Hobza (1♀, UCR). NEVADA: **Clark:** Cabin Creek S Mequite, 15 May, FDP (1♀, USU). **Mineral:** 5 mi NW Schurz, 15 June, R. C. Bechtel and J. P. Young (1♀, CAS; 2♀, NSDA). TEXAS: **Culberson:** 26 km N Van Horn, 9 Apr, TLG (2♂, CAS, USU).

MEXICO: **Baja California Norte:** Angeles Bay, 26 June, E. P. Van Duzee (1♀, CAS); San Quintin, 24 May, FXW (1♀, CAS). **Baja California Sur:** 4 mi WSW Miraflores, J. Slansky, M. K. and C. Wasbauer (5♀, 2♂, CAS; 6♀, 2♂, CSDA); same locality, MSW (2♀, CSDA). **Durango:** 5 mi E Coyotes, 4 Aug, HEE (1♀, MCZ).

Tachysphex hurdi R. Bohart

(Figures 77, 78)

Tachysphex hurdi R. Bohart, 1962:33, ♂, ♀, ! Holotype: ♂, California: Ventura Co.: Hungry Valley 5 mi S Gorman (CAS).—Krombein 1967:393; Bohart and Menke 1976:274; Krombein 1979:1628

DIAGNOSIS.—*Tachysphex hurdi* has a black body, well-defined mesopleural punctures, sternum I without apical depression, and in most specimens, the midscutal setae are oriented almost uniformly posterad. Some *psammobius* (those with an all black gaster) are similar, but their length is 6–7 mm (female) or 4.5–5.5 mm (male), and the male clypeal lip is triangular. The body length of *hurdi* is 8.5–11 mm (female) or 7–11 mm (male), and the male clypeal lip is variously shaped (Fig. 77b), but not triangular. *Tachysphex glabrior* is also similar, but the vertex setae of *hurdi* (erect, 1.5 MOD long) are distinctive. Unlike *papago, psilocerus,* and *scopaeus,* tergum I of *hurdi* is sculptured and pilose throughout. Unlike the Old World *tarsinus* (Lepeletier), the clypeal lip of female *hurdi* has a mesal projection, and the forefemoral notch of most males is glabrous.

DESCRIPTION.—Frons dull or shiny. Vertex width 1.3–1.5× length. Scutum shiny. Punctures deep, well-defined on frons, vertex, and mesothorax, subcontiguous to one diameter apart on frons; slightly more to slightly less than one diameter apart on vertex; less than one diameter apart on scutum (many discal punctures sometimes one diameter apart); less than one diameter apart on mesopleuron (one to two diameters apart posteriorly). Propodeal dorsum rugose, side and hindface ridged. Discal punctures on tergum II more than one diameter apart. Sternum I evenly convex apically, apical depression narrow, hardly visible. Hindcoxa finely ridged along inner margin.

Vestiture not obscuring integument between antennal socket and orbit. Setae erect, 1.5 MOD long on vertex; on scutum suberect, 0.8–0.9 MOD; appressed or suberect (and then almost 1.0 MOD long apically) on midfemoral venter.

Body black, tarsal apex brownish, reddish in most males. Terga I–III or I–IV silvery fasciate apically. Wings slightly infumate to hyaline.

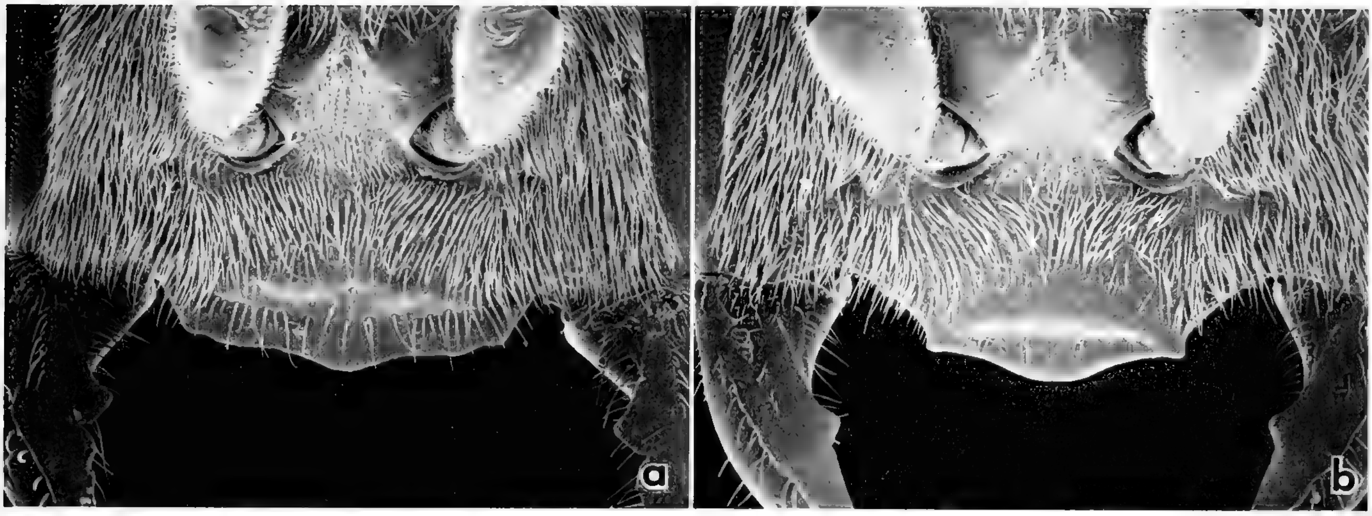

FIGURE 77. *Tachysphex hurdi* R. Bohart: a—female clypeus; b—male clypeus.

♀.—Clypeus (Fig. 77a): bevel swollen to scarcely concave, equal to basomedian area or shorter; lip weakly arcuate, with short, obtuse projection mesally, not incised laterally. Dorsal length of flagellomere I 1.7–2.2× apical width. Tergum V punctate, apical depression impunctate. Trochanters and forefemora finely, densely punctate. Length 8.5–11.0 mm.

♂.—Mandibular inner margin with tooth (Fig. 77b). Clypeus (Fig. 77b): bevel semilunate, distinctly delimited from basomedian area, much shorter than latter, slightly concave to swollen; lip foremargin straight, slightly concave, or sinuate; its corners prominent, as close to orbit as to each other (slightly less in some specimens). Dorsal length of flagellomere I 1.2–1.7× apical width. Sterna punctate throughout. Forefemoral notch glabrous in most specimens, but pruinose in a male from Willow Wash, San Bernardino Co., California (TLG). Foretarsus without rake; outer apical spine of tarsomere II much shorter than tarsomere III. Length 7–11 mm.

VARIATION.—The scutal setae are oriented almost uniformly posterad in most specimens, but the midscutal setae are oriented posterolaterad in a female from the Bonanza area, Utah (USU).

In most specimens, sternal punctures are inconspicuous, finer than those on the mesothoracic venter. They are conspicuous, larger than those on the mesothoracic venter in the following specimens: Arizona: Cochise Co.: 2 mi W Portal (1♂, CAS), Southwestern Research Station 4 mi SW Portal (1♀, 2♂, UCD); Pinal Co.: Boyce Thompson Arboretum 3 mi W Superior (1♀, CAS); county unknown: Oak Creek Canyon (1♀, 1♂, UCD); California: Inyo Co.: Darwin Falls (1♂, UCD); Surprise Canyon in Panamint Mts. (1♂, UCD); Utah: Washington Co.: Paradise Canyon (1♀, USU), Snow Canyon (1♀, CAS; 2♀, 1♂, USU).

Specimens from Mexico, California, Idaho, Madera Canyon, Arizona, and Reno, Nevada, have silvery fasciate apically terga I–III, slightly infumate wings, and an impunctate pygidial plate of the female. A female from Bumble Bee, Arizona (UCD) and specimens from Snow Canyon, Utah, are similar, except for the silvery fasciate tergum IV. A female from Sycamore Canyon, Arizona (USU), and another one from Paradise Canyon, Utah (USU), have fasciate terga I–IV, weakly infumate wings, and their pygidial plate is punctate laterally. A female from Boyce Thompson Arboretum, Arizona (CAS) and one from Lagomarsino Canyon, Nevada (NSDA), have silvery fasciate apically terga I–IV, infumate wings, and an impunctate pygidial plate.

GEOGRAPHIC DISTRIBUTION (Fig. 78).—Idaho, Oregon, and Utah to Arizona, and Baja California Norte.

MATERIAL EXAMINED.—95♀, 159♂ (including 23♀, 37♂ paratypes).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** 2 mi W Portal, Southwestern Research Station (4 mi SW Portal). **Mohave:** Kingman. **Pima:** Madera Canyon in Santa Rita Mts. **Pinal:** Boyce Thompson Arboretum 3 mi W Superior. **Santa Cruz:** Sycamore Canyon. **Yavapai:** Bumble Bee. **County unknown:** Oak Creek Canyon. CALIFORNIA: **Alameda:** Arroyo Mocho. **Alpine:** Silver Creek. **Amador:** Volcano. **El Dorado:** Chili Bar. **Fresno. Humboldt:** 5 mi NW Garberville, Mad River Beach, Southern Fork of Eel River. **Inyo. Kern:** Antelope Canyon near Tehachapi, Mill Potrero, Rancheria Creek (Piute Mts.). **Lassen:** Hallelujah Junction. **Los Angeles. Madera:** Madera. **Mariposa:** Usona. **Mendocino:** 7 mi E Eel River Ranger Station, Mayacamas Mts., Robinson Creek (4 air mi SW Ukiah). **Mono. Monterey:** Arroyo Seco Camp, Monterey, Pacific Grove. **Nevada:** 10 air mi NNW Nevada City. **Riverside. San Benito:** Idria. **San Bernardino. San Diego. San Luis Obispo:** 4 mi SE Santa Margarita (also 6 mi NE). **Santa Barbara:** Bluff Camp (San Rafael Mts.), Los Prietos (also 4 mi E). **Santa Clara:** San Antonio Ranger Station. **Shasta:** Cassel, Hat Creek Post Office. **Sierra:** Sattley, Sierra Valley. **Siskiyou:** Upper Devils Peak. **Stanislaus:** Del Puerto Canyon. **Trinity:** Hayfork, Ruth. **Tulare:** California Hot Springs, Camp Wishon, Three Rivers. **Ventura:** Hungry Valley (5 mi S Gorman), Quatal Canyon (NW corner of county), Wagon Road No. 2 Campground (18 air mi WSW Gorman). IDAHO: **Gooding:** 1 mi NE Gooding. **Washington:** 32 mi W Indian Valley. NEVADA: **Storey:** Lagomarsino Canyon. **Washoe:** Reno. OREGON: **Wasco:** 5 mi S Dufur. UTAH: **Bonanza:** SW Bonanza. **Washington:** Paradise Canyon, Snow Canyon.

MEXICO: **Baja California Norte:** 3.9 mi S El Cóndor, Ensenada, Descanso, Santo Domingo area, 10 mi NW Santo Tomás. **Baja California Sur:** 3.5 km WNW San Isidro.

Tachysphex psammobius (Kohl)

(Figures 79, 80)

Tachytes psammobia Kohl, 1880:235, ♂, ♀ (incorrect original spelling). ! Lectotype ♀, Italy: Bolzano (Naturhist. Mus. Vienna, Austria), designated by Pulawski 1971:189.—In *Tachysphex*: Kohl 1885:386; Pulawski 1971:189 (bibliography and summary of data on Palearctic populations); Bohart and Menke 1976:276, Kurczewski 1987:121.

Tachysphex asperatus W. Fox, 1894*a*:516, ♀. ! Holotype: ♀, Nevada: no specific locality (ANSP). Synonymized with *sculptilis* by Pulawski *in* Krombein 1979: 1629.—Dalla Torre 1897:678; Ashmead 1899:250; Cresson 1928:43; G. Bohart 1951:950; Bohart and Menke 1976:272.

Tachysphex sculptilis W. Fox, 1894*a*:517, ♀. ! Holotype: ♀, Colorado: no specific locality (ANSP). **New synonym.**—Dalla Torre 1897:685; Cresson 1928:46; G. Bohart 1951:952; Bohart and Menke 1976:276; Krombein 1979:1629.

Tachysphex nigrescens Rohwer, 1908:220, ♀. ! Holotype: ♀, Colorado: Teller Co.

FIGURE 78. Geographic distribution of *Tachysphex hurdi* R. Bohart.

Florissant (USNM). Synonymized with *sculptilis* by Pulawski *in* Krombein 1979:1629. — G. Bohart 1951:951. Bohart and Menke 1976:274.

Tachysphex sphecodoides Rohwer, 1911:578, ♀, ! Holotype: ♀, Colorado: Otero Co.: Rocky Ford (USNM). Synonymized with *sculptilis* by G. Bohart 1951:952.

DIAGNOSIS.—*Tachysphex psammobius* can be recognized by its small size (4.5–7.0 mm) combined with the punctate mesopleuron, midscutal setae oriented posterad or posterolaterad, presence of short, erect setae on the vertex and on the midfemoral venter apically (Fig. 79b); femoral setae suberect in male. The mesopleural punctures are ill defined in some males that can be recognized by the femoral setae character combined with the triangular clypeal lip (Fig. 79c), nondentate inner mandibular margin (Fig. 79c), nonvelvety sternal pubescence, and the rugose or ridged propodeal dorsum.

DESCRIPTION.—Frons, vertex, and mesothorax punctate; frontal and mesopleural punctures less than one diameter apart but mesopleural punctures often evanescent or more than one diameter apart posteriorly, ill defined in some males; interspaces dull or glossy. Propodeal dorsum irregularly rugose to longitudinally ridged; side ridged or (occasional specimens) ridges largely evanescent; hindface ridged, margined above. Discal micropunctures of tergum II two to several diameters apart. Sternum I without apical depression. Hindcoxa not carinate.

Vestiture not obscuring integument between antennal socket and orbit. Vertex setae erect, about 1.1–1.5 MOD long (but see also Variation below); midscutal setae oriented posterad.

Head, thorax, and legs black, tarsal apex brown. Gaster red to black. Wings faintly infumate. Frontal vestiture silvery.

♀.—Clypeus (Fig. 79a): bevel shorter to longer than basomedian area; lip arcuate or sinuate, not emarginate mesally or incised laterally. Dorsal length of flagellomere I 1.9–2.1 × apical width. Vertex width 1.5–1.6 × length. Punctures one to two diameters apart on vertex (rarely less), less than one diameter apart on scutum (rarely one or two diameters); minute on tergum V (apical depression impunctate). Pygidial plate alutaceous, sparsely punctate. Trochanteral and femoral punctation fine, dense, but trochanteral punctures sometimes evanescent. Length 6–7 mm.

Setae 0.3–0.4 MOD long on scutum, on midfemoral venter erect (Fig. 79b), about 1.0 MOD long distally (see also Variation below).

Terga I–IV silvery fasciate apically, fasciae usually weak.

♂.—Inner mandibular margin not dentate (Fig. 79c). Clypeus (Fig. 79c): bevel shorter than basomedian area, indistinctly delimited from the latter; lip obtusely triangular, its corners obtuse, indistinct, about as close to orbit as to each other. Dorsal length of flagellomere I 1.1–1.5 × apical width. Vertex width 1.6–2.2 × length. Punctures subcontiguous on scutum, about one diameter apart on vertex; minute on sterna (some of them more than one diameter apart); apical depression of sterna II and III partly impunctate in some specimens. Forefemoral notch glabrous or pruinose. Forebasitarsus usually without preapical rake spines, rarely with one or two spines (that are as long as width of basitarsus); outer apical spine of foretarsomere II about as long as tarsomere width. Length 4.5–6.3 mm.

Setae usually 0.5–0.6 MOD long on scutum, on midfemoral venter suberect, 0.3–0.8 MOD long on apical half (see also Variation below).

Terga I–V silvery fasciate apically.

VARIATION.—Body vestiture is longer in many specimens from southeastern Arizona, New Mexico, southwestern Texas (El Paso), and northwestern Texas (Turkey area) than it is in other individuals. For example, the vertex setae are (in MOD) 1.7

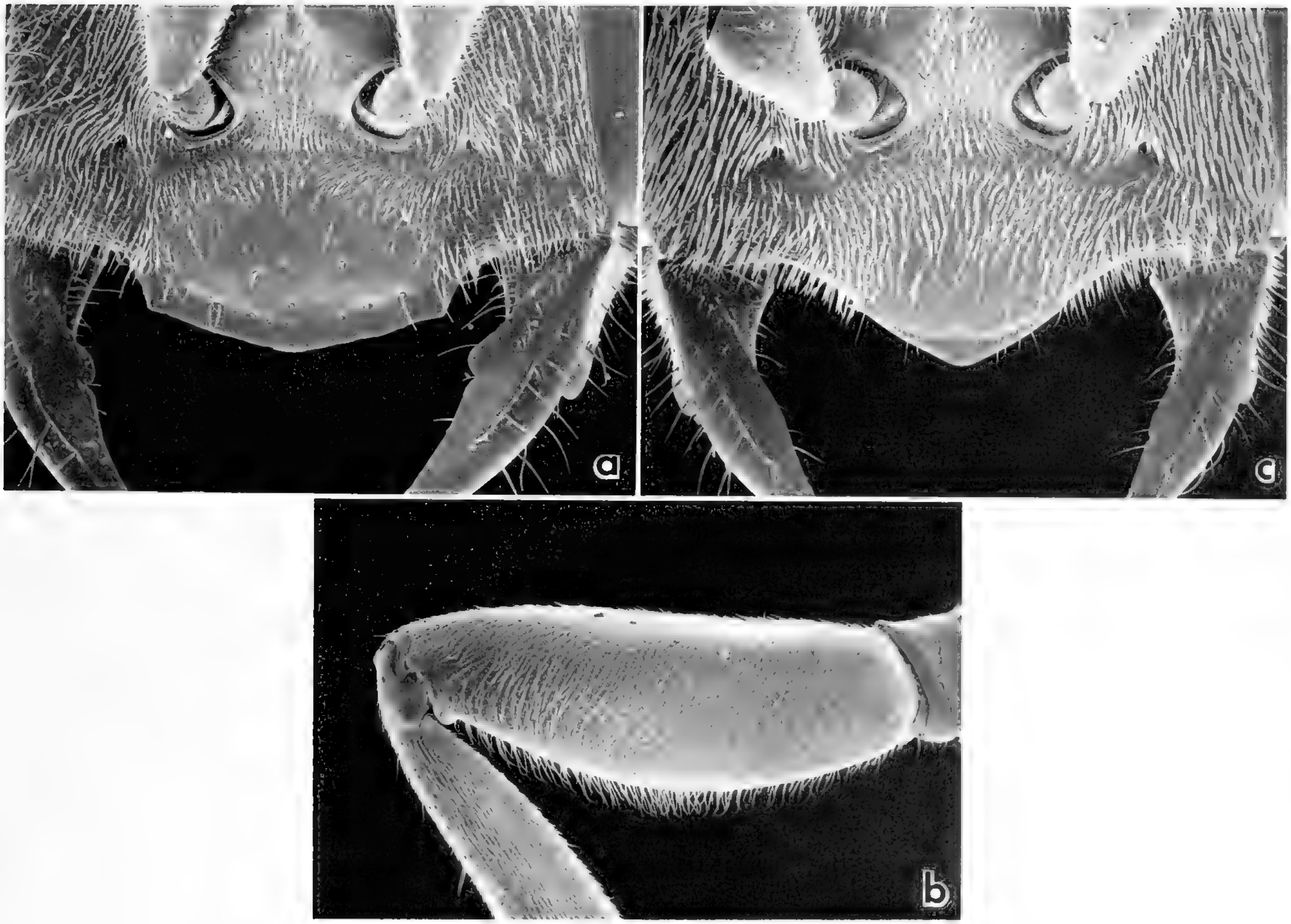

FIGURE 79. *Tachysphex psammobius* (Kohl): a—female clypeus; b—female midfemur; c—male clypeus.

long in a female from Picacho (MCZ) and 1.0 in one from Tucson (UCD), and the midfemoral setate are 1.3 long apicoventrally in two females from Willcox area (UCD) and in one from El Paso (UCD). The midfemoral setae are 1.0 MOD long in a male from Paradise Camp, California (UCD). Specimens with unusually long vestiture have a glossy mesopleuron.

In specimens from Valentine, Texas (1♀, 1♂, UCD), the mesopleural punctures are coarse, the interspaces are glossy, and the body vestiture is unusually long. The length of setae is 2.0 MOD on the vertex, on the scutum anteriorly, and on the mesopleuron, and 1.3–1.5 MOD on the midfemoral venter distally. In spite of these differences, I regard these individuals as *psammobius* rather than a distinct species.

LIFE HISTORY.—Nothing was known about the life history of *psammobius*, either in Europe or in North America, until Kurczewski (1987) observed a female near Manhattan, Kansas. Early instars of the grasshopper *Melanoplus*, either *differentialis* Thomas or *sanguinipes* (Fabricius), were used as prey and carried to the nest in flight. One prey was malaxated after stinging. During transport, the wasp clasped the grasshopper's body with all her legs and held the antennal bases with her mandibles. The wasp either took the prey directly into the nest or first dropped it at the entrance (she then entered the burrow, turned around inside, reappeared headfirst, and pulled the prey in). The description implies that the nest was permanently open during the provisioning period. She took an orientation flight after bringing in the first prey. Eleven prey were deposited in the cell, all head inward, nine venter up and two dorsum up. The egg was laid on the right forecoxal corium of the second largest prey and extended transversely between the fore- and midcoxae. The nest consisted of an oblique burrow and a single cell, with a tumulus near the entrance. After provisioning was completed, the wasps first used her forelegs in unison for closing the nest, and then packed the sand with the tip of her abdomen. Kurczewski (1987) also mentioned a female from Yuba Pass, California (UCD), pinned with her prey, a nymphal acridid *Aerochoreutes maculatus* (Scudder).

GEOGRAPHIC DISTRIBUTION (Fig. 80).—*Tachysphex psammobius* is a Holarctic nondesert species, although it occurs mainly in sandy habitats. In the New World, it ranges between British Columbia and western Texas, west to California, east to Nebraska and Colorado. In the Old World, it occurs in Europe.

FIGURE 80. Geographic distribution of *Tachysphex psammobius* (Kohl) in North America

Cyprus, Turkey, Transcaucasia, Transcaspia, and in Siberia (Irkutsk area). It has not been found in the British Isles, Denmark, Fennoscandia, and Russia north of 59°N.

MATERIAL EXAMINED.—201♀, 133♂.

RECORDS (b: gaster black).—CANADA: **British Columbia:** Oliver (b), Osoyoos (b), Skihist Camp on Fraser River (b)

UNITED STATES: ARIZONA: **Cochise:** Portal (also 3, 5, and 6 mi W, 3 mi SW, 3 mi E, 30 mi S). **Maricopa:** Rainbow Valley, route 74 5 mi W route 17 (partly b). **Pima:** Santa Catalina Mts., Tucson. **Pinal:** Picacho. **Santa Cruz:** Nogales, Tubac. CALIFORNIA: **Alameda. Alpine:** Hope Valley, Winnemucca, Woods Lake. **Colusa:** Walker Ridge (2 mi W Leesville). **Contra Costa. El Dorado. Fresno:** 1 mi E Frypan Meadow, Volcanic Lakes (b). **Humboldt:** 2 mi W Briceland, 3 mi N Garberville, Kneeland. **Inyo:** Grapevine Canyon (b). **Kern:** Glenville, 1 mi W Tehachapi. **Lassen:** 6 mi S Doyle. **Los Angeles:** 15 mi E Gorman, Tanbark Flat. **Marin:** Mt. Tamalpais State Park. **Mariposa:** 1 mi E Jerseydale. **Modoc. Mono. Monterey:** Arroyo Seco, Bryson. **Napa:** Angwin. **Nevada:** Boca, Sagehen Creek near Hobart Mills (partly b). **Orange:** Trabuco Canyon. **Placer. Plumas:** Buck's Lake. **Riverside:** Sage. **Sacramento:** 10 mi NE Folsom. **San Benito:** 4 mi S Mercy Hot Springs (in Fresno Co.). **San Bernardino:** Mid Hills (9 mi SSE Cima), 1 mi W Needles. **San Diego:** Guatay. **San Luis Obispo:** Pozo (also 12 mi NE). **Santa Barbara:** Santa Ynez Mts. **Sierra:** Yuba Pass near Sierraville. **Siskiyou. Trinity:** Hayfork. **Tulare:** Sequoia National Park, Visalia. **Tuolumne:** Buck Meadows, 3 mi W Sonora Pass (partly b). **Yolo:** Cache Creek Canyon, Davis. COLORADO: **Larimer:** Hewlett Gulch. **Las Animas:** —. **Otero:** Rocky Ford (b). **Teller:** Florissant (b). IDAHO: **Blaine:** 5 mi N Chinook Mt. (b). **Custer:** 25 mi W Mackay. **Franklin:** Cub River Canyon (b). **Gooding:** 5 mi N Bliss, Hagerman Valley, Wood River 1 mi NE Gooding. **Lemhi:** 3 mi E Baker (b), Lemhi Pass (b). **Oneida:** Black Pine Canyon. **Owyhee:** Given Springs. MONTANA: **Sheridan:** Medicine Lake. NEBRASKA: **Blaine:** Dunning (b). NEVADA: **Elko:** Angel Lake in E Humboldt Range (b), Lamoille Canyon (Ruby Mts.). **Eureka:** Eureka. **Washoe:** Galena Creek, Mt. Rose summit (partly b). NEW MEXICO: **Dona Ana:** 12 mi N Las Cruces. **Roosevelt:** Oasis State Park. **Sierra:** Percha Dam State Park. OREGON: **Crook:** 9.5 mi N Post. **Jackson:** 6 mi NW Medford. **Jefferson:** Cove State Park (5 mi NW Culver—b). **Klamath:** above Algoma, Buck Lake Road 2.5 mi N Highway 66, 3 mi N Gearhart Mt., Klamath Falls. TEXAS: **El Paso:** El Paso. **Hall:** 6 mi SE Turkey. **Jeff Davis:** Valentine. UTAH: **Beaver:** Beaver Canyon. **Box Elder:**—. **Cache:** Blacksmith Fork, Herd Hollow, Logan, Logan Canyon, Sardine Canyon. **Garfield:** Calf Creek. **Juab:** Nephi. **Weber:** Willard Peak. WASHINGTON: **Whitman:** Pullman (b). WYOMING: **Fremont:** Lander (partly b). **Natrona:** Pathfinder Dam (8 air mi SW Alcova—b). **Teton:** 6 mi N Jackson, Moran (partly b).

Tachysphex glabrior Williams

(Figures 81, 82)

Tachysphex glabrior Williams, 1914:170, ♀, ♂. Holotype: ♀, Kansas: Phillips Co.: no specific locality (?KU, see Discussion below).—Mickel 1918:423; G. Bohart 1951:951; LaBerge 1956:527; Arnaud 1970:32; Bohart and Menke 1976:275 (incorrectly synonymized with *Tachysphex mundus* by R. Bohart); Krombein 1979:1628.

DIAGNOSIS.—*Tachysphex glabrior* has a shiny, punctate mesopleuron, scutal setae are oriented uniformly posterad, and sternum I is not depressed apically. These traits are shared with some other species. Unlike *papago, psilocerus,* and *scopaeus,* terga I and II of *glabrior* are microsculptured throughout. Like *crenulatus* and *verticalis* (which have an impunctate mesopleuron), the clypeal lip of the female has two lateral incisions on each side (Fig. 81a); the presence of graduli on female sternum III is a subsidiary recognition feature. The male can be recognized by the presence of the graduli on sterna III–V (if sterna are fully extended); the combination of vertex setae that are 0.3–0.6 MOD long and of an arcuate or sinuate clypeal lip is also distinctive (vertex setae more than 1.0 MOD long in *hurdi* and *psammobius,* clypeal lip triangular in *psammobius*).

DESCRIPTION.—Frons shallowly, evenly punctate or (some males) microsculptured; punctures subcontiguous or (some specimens) several punctures before midocellus slightly more

FIGURE 81. *Tachysphex glabrior* Williams: a—female clypeus; b—male clypeus.

than one diameter apart. Vertex evenly punctate, punctures less than one to about two diameters apart. Mesothorax shiny. Scutal punctures well defined, less than one diameter apart or (some specimens) a few discal punctures slightly more than one diameter apart. Mesopleural punctures fine, less than one diameter apart, but in most specimens two to three diameters apart posteriorly. Propodeal dorsum irregularly rugose or microreticulate; side and hindface ridged. Discal micropunctures of tergum II one to two diameters apart. Sternum I without apical depression. Hindcoxa carinate.

Vestiture almost totally hiding sculpture between antennal socket and orbit. Setae erect or suberect on vertex, 0.3–0.6 MOD long; subappressed on scutum and midfemoral venter, 0.3–0.5 MOD long; midscutal setae oriented posterad.

Body black with black tarsal apex or (some females) gastral segments I–III predominantly red. Wings weakly infumate to almost hyaline. Terga I–IV (I–V in many males) silvery fasciate apically. Frontal vestiture silvery.

♀.—Clypeus (Fig. 81a): bevel evenly swollen, equal to basomedian area or shorter; lip weakly arcuate to almost straight, with two lateral incisions on each side. Dorsal length of flagellomere I 1.5–1.7 × apical width. Vertex width 1.1–1.3 × length. Tergum V densely to sparsely punctate, apical depression impunctate. Pygidial plate punctate. Sternum III with graduli. Trochanters minutely, closely punctate. Forefemoral venter micropunctate, punctures one to three diameters apart. Length 6.5–7.5 mm.

♂.—Mandibular inner margin with tooth (Fig. 81b). Clypeus (Fig. 81b): bevel triangular, shorter than basomedian area; lip broadly arcuate or sinuate, weakly pointed mesally; its lateral corners distinct, obtuse; distance between corners about 1.25 of clypeal midline, and about 1.25 of distance between corner and orbit. Dorsal length of flagellomere I 1.0–1.25 × apical width. Vertex width 1.3–2.2 × length. Sterna densely punctate throughout, sterna III–V with graduli. Forefemoral notch finely pubescent. Foretarsus without rake; outer apical spine of tarsomere II much shorter than tarsomere III. Length 4.5–6.5 mm.

VARIATION.—The gaster is black in most specimens examined, but segments I–III are predominantly reddish in two of the six females examined from Bentsen Rio Grande Valley State Park, Texas (CAS). It is all red in a female from Cintalapa area, Mexico (UCD).

DISCUSSION.—The specimen of *glabrior* (KU) labeled holotype by F. X. Williams bears the label "Ness Co., Kansas." Phillips Co. was given as type locality in the original description, and there is a discrepancy in the collecting dates. Therefore, the presumed type may not be the true type. Possibly Williams (1914) gave the wrong type locality or the original labels were subsequently changed.

GEOGRAPHIC DISTRIBUTION (Fig. 82).—Kansas, Texas, Oklahoma, and southeastern Arizona to northwestern Venezuela.

MATERIAL EXAMINED.—58♀, 28♂ (CAS, CSU, CU, FSCA, KU, MCZ, KVK, UCD, UCR, UMMZ, USNM)

RECORDS.—UNITED STATES: ARIZONA: **Santa Cruz:** Santa Rita Mts. (1♀, KU). KANSAS: **Ellis, Ness:** —. Also Osborne, Phillips, Pratt, and Rush counties according to Williams (1914), but a male from the Rush Co. labeled as *glabrior* by him is actually *antennatus*. OKLAHOMA: **Comanche:** Wichita National Forest. TEXAS: **Bosque:** Meridian State Park. **Brazos:** —. **Brown:** Lake Brownwood State Park. **Cameron:** 13.4 and 15 mi E Brownsville. **Crockett:** Fort Lancaster State Historical Park. **Guadalupe:** Seguin. **Hidalgo:** Bentsen Rio Grande Valley State Park, McAllen Botanical Garden. **Kimble:** Junction. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **Lee:** Fedor. **Palo Pinto:** Possum Kingdom State Park. **Somervell:** Dinosaur Valley State Park. **Travis:** Austin

MEXICO: **Chiapas:** 25 mi W Cintalapa. **Jalisco:** Estanzuela (40 km W Ameca) **Morelos:** Cuernavaca (also 3 mi NW). **Nayarit:** Ixtlán del Río. **Puebla:** Petlalcingo **San Luis Potosi:** 5 mi N Ciudad del Maiz. **Sonora:** Alamos

CENTRAL AMERICA: COSTA RICA: Bebedro and Río Corbici near Cañas in Guanacaste Province. EL SALVADOR: Hacienda Capolinas (5 km NW Quezaltepeque), Quezaltepeque, San Salvador. HONDURAS: Zamorano

VENEZUELA: **Aragua:** Lago de Valencia. **Zulia:** 31 km SW Machiques

Tachysphex oasicola sp. n.

(Figures 82, 83)

DERIVATION OF NAME.—The name *oasicola* is derived form the Latin word oasis, and the suffix -cola, a dweller; a reference to Oasis State Park in New Mexico, where the holotype was collected.

DIAGNOSIS.—*Tachysphex oasicola* is characterized by a con-

FIGURE 82. Geographic distribution of *Tachysphex glabrior* Williams and *oasicola* sp. n.

spicuously punctate mesopleuron and transversely oriented midscutal setae. *Tachysphex texanus* and its relatives have the same characters, but *oasicola* differs in having sternum I barely depressed apically. Helpful recognition features, although found in many other *Tachysphex,* are the sparsely punctate scutal disk (see Description below for details) and the red hindfemur (at least in the female). The sinuate clypeal lip of the female (Fig. 83a) is unique, and the shape of the male clypeus (Fig. 83b) is diagnostic in combination with the features mentioned above.

DESCRIPTION.—Punctures nearly contiguous on frons or (Texan females) more than one diameter apart; averaging several diameters apart on vertex except less than one diameter apart on postocellar impression; several to many diameters apart on scutal disk (except close to each other on area with transversely oriented setae); conspicuous and well defined on mesopleuron, averaging about two diameters apart beneath mesopleural scrobe; unevenly distributed on mesothoracic venter (less than one to more than two diameters apart). Propodeal dorsum irregularly microrugose, longitudinally ridged; side and hindface ridged; hindface ridges larger and farther apart than in other North American species. Sternum I with ill-defined apical depression. Discal punctures of tergum II a few diameters apart. Hindcoxa carinate basally.

Vestiture totally concealing sculpture between antennal socket and orbit as seen from many angles. Setae erect on vertex, slightly more than 1.0 MOD long; transversely oriented on midscutum; inclined on mesopleuron; appressed on midfemoral venter.

Head and thorax black, gaster red. Gastral terga I–III weakly fasciate apically, also tergum IV apicolaterally. Wings hyaline. Frontal vestiture silvery.

♀.—Clypeus (Fig. 83a): bevel about as long as basomedian area; lip weakly sinuate, not incised laterally. Dorsal length of flagellomere I 2.0 × apical width. Vertex width 1.0–1.1 × length. Tergum V with a few, sparse punctures; apical depression impunctate. Pygidial plate alutaceous, sparsely punctate. Trochanters and femora finely, densely punctate. Length 9–10 mm.

Forefemur black, or red apically; midfemur black except reddish apically or (Texas females) also ventrally; hindfemur largely red (base and basodorsal third black), nearly all red in Texan females. Foretibia black, reddish on inner side; midtibia black except red on apical third, or red except black basally; hindtibia red except black at its very base. Tarsi red.

♂.—Mandibular inner margin with tooth. Clypeus (Fig. 83b): bevel shorter than basomedian area; lip sinuate, its base straight, its lateral corner well defined; distance between corners equal to 0.7 of clypeal length and of distance between a corner and orbit. Dorsal length of flagellomere I 1.6 × apical width. Vertex width 1.4 × length. Sterna punctate, except impunctate apical depressions of sterna II–V. Forefemoral notch pruinose. Forebasitarsus with one to three preapical rake spines. Outer apical spine of foretarsomere II shorter than tarsomere width. Length 6.5–7.5 mm.

Fore- and midfemora black; hindfemur largely red (black on basodorsal half) in holotype, black except red on apical third in paratype. Foretibia black, red on inner side; midtibia largely black with variable amount of red; hindtibia largely red (black basally) in holotype, black with small red areas apically in paratype. Tarsi red.

GEOGRAPHIC DISTRIBUTION (Fig. 82).—Western Texas, New Mexico, Wyoming.

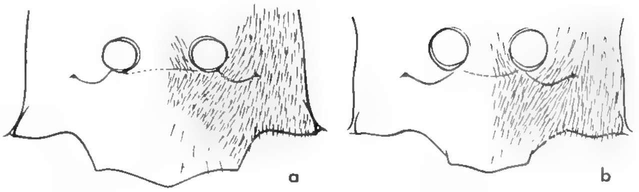

FIGURE 83. *Tachysphex oasicola* sp. n.: a—female clypeus; b—male clypeus.

MATERIAL EXAMINED.—Holotype: ♂, New Mexico: Roosevelt Co.: Oasis State Park, 21 May 1985, WJP (CAS, Type #15904).

Paratypes (3♀, 1♂): UNITED STATES: NEW MEXICO: **Roosevelt:** 1♂, same data as holotype. TEXAS: **Culberson:** 60 mi N Van Horn, 9 Apr 1986, TLG (2♀, CAS, USU). WYOMING: **Uinta:** Evanston, 4 Sept 1966, A. Wilkins (1♀, CAS).

Tachysphex amplus W. Fox

(Figures 84, 85)

Tachysphex amplus W. Fox, 1894*a*:522, ♀, ♂. ! Lectotype: ♀, Nevada: no specific locality (ANSP), designated by Cresson 1928:43.—Dalla Torre 1897:678; Ashmead 1899:250; Cockerell 1900:143; G. Bohart 1951:950; Krombein 1967:392; Bohart and Menke 1976:272; Krombein 1979:1627; Rust et al. 1985:46.

Tachysphex gillettei Rohwer, 1911:571; ♀. ! Holotype: ♀, Colorado: Rocky Ford (USNM). Synonymized by G. Bohart 1951:950

Tachysphex neomexicanus Rohwer, 1911:575, ♀. ! Holotype: ♀, New Mexico: Rio Ruidoso in White Mts. (USNM). Synonymized by G. Bohart 1951:950

DIAGNOSIS.—*Tachysphex amplus* has a punctate mesopleuron and transversely oriented midscutal setae. Several other species share these characters, but they have a horizontal depression at the apex of sternum I, while *amplus* has a triangular, gradually sloping surface (Fig. 84b), which in most specimens is slightly concave. The shape of the clypeal lip in both sexes (Fig. 84a, c) and the long male flagellomere I (dorsal length 1.7–2.0 × apical width; Fig. 84d), are also distinctive. Subsidiary diagnostic features are: body large (female: 11–13 mm, male: 8.5–10.0 mm), and male sterna with velvety pubescence.

DESCRIPTION (see also Table 2 under *texanus,* p. 123).—Punctures less than one to slightly more than one diameter apart on vertex; on scutum mainly subcontiguous, but up to three diameters apart on disk in some specimens. Mesopleural punctures 0.3–2.0 diameters apart below scrobe. Propodeal dorsum coarsely rugose, not ridged, or (some specimens) microareolate or very densely punctate. Discal micropunctures of tergum II two to five diameters apart.

Vertex setae about 1.0 MOD long.

Legs in most specimens black (except tarsal apex reddish), but part of hindfemur or all femora and part of hindtibia red in occasional Arizona and California females. Gaster red, rarely male segments V–VII brown. Terga I–III or I–V silvery fasciate apically, fascia interrupted mesally. Wings almost hyaline.

♀.—Clypeus (Fig. 84a): bevel about as long as basomedian area; lip arcuate, narrow or (some specimens) broadened mesally. Dorsal length of flagellomere I 2.2–2.5 × apical width. Vertex width slightly more to slightly less than length. Tergum V sparsely punctate. Length 11–13 mm.

Vestiture not obscuring integument between antennal socket and orbit. Scutal setae appressed or suberect, shorter than MOD.

♂.—Clypeus (Fig. 84c): lip straight to arcuate, its corners distinct, closer to each other than to orbits (markedly so in some specimens) or equidistant; short, longitudinal carina extending from each lip corner. Dorsal length of flagellomere I (Fig. 84d) 1.7–2.0 × apical width. Vertex width 1.3–1.5 × length. Tergum

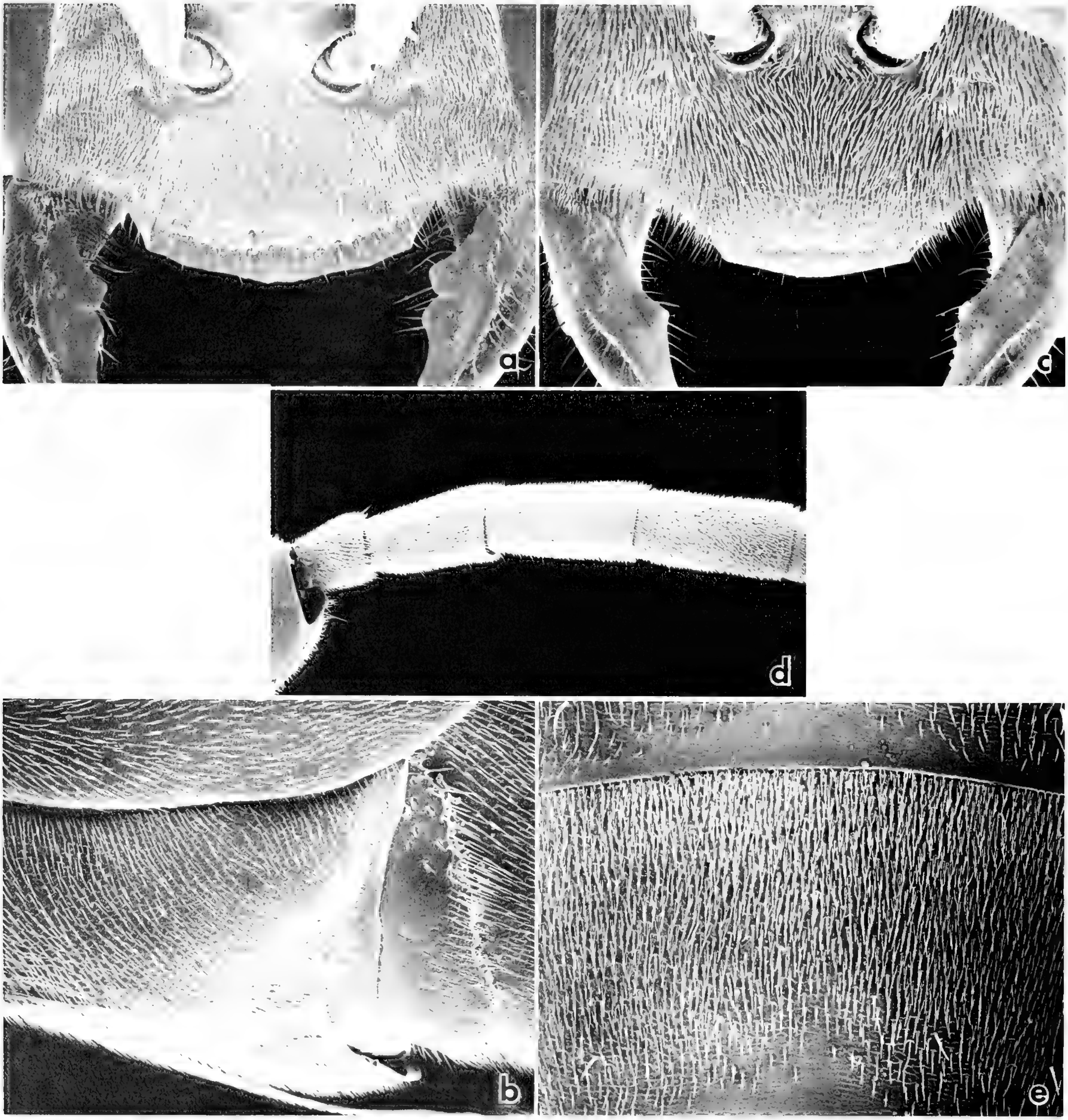

FIGURE 84. *Tachysphex amplus* W. Fox. a—female clypeus, b—female sternum I obliquely; c—male clypeus; d—basal flagellomeres of male; e—vestiture of male sternum III.

VII densely punctate except basal punctures sometimes more than one diameter apart. Sterna II–VII evenly, minutely punctate (punctures less than one diameter apart), except for smooth, impunctate apical depression. Length 8.5–11.0 mm.

Vestiture obscuring integument between antennal socket and orbit (except when viewed from certain angles). Scutal setae subappressed, about 1.0 MOD long. Sternal pubescence velvety, almost concealing integument (Fig. 84e).

GEOGRAPHIC DISTRIBUTION (Fig. 85).—United States and Mexico west of 100th meridian, north to southern Alberta.

MATERIAL EXAMINED.—255♂, 439♀.

RECORDS.—CANADA. **Alberta**: Pakowki Lake

UNITED STATES: ARIZONA: **Apache:** Canyon de Chelly, 10 mi W Springerville. **Cochise. Coconino:** Flagstaff, 6,700 ft. **Maricopa:** Wickenburg. **Mohave:** 9 mi E Oatman, Peach Springs. **Navajo:** Jadito Trade Post. **Pima:** 12 mi W Tucson. **Pinal:** Casa Grande. **Santa Cruz:** Canelo, Madera Canyon (Santa Rita Mts.), Sonoita. **Yavapai:** Oak Creek near Cornville. CALIFORNIA: **Alameda:** Livermore, Sycamore Grove State Park. **Alpine:** 3 mi NE Woodfords. **Colusa:** Little Stony Creek. **Contra Costa:** Antioch, Mount Diablo, 5 mi SE Walnut Creek. **El Dorado:** 10 mi N on Ice House Road. **Fresno. Glenn:** Artois. **Humboldt:** 4 mi E Alderpoint. **Inyo. Kern. Lake:** Lake Pillsbury, Middletown. **Lassen:** Constantia, Hallelujah Junction, Hot Spring Mountain. **Los Angeles. Marin:** Larkspur (Baltimore Park). **Mariposa:** Yosemite Valley. **Mendocino:** Hopland Field Station, Robinson Creek (4 air mi SW Ukiah). **Modoc:** Alturas. **Mono. Monterey. Napa:** 5.5 km NW Moscowite Corner (Capell Creek), Napa. **Orange:** Corona del Mar, Laguna Beach. **Placer:** Auburn, Roseville. **Riverside:** 16 mi N Blythe, Deep Canyon, Riverside. **Sacramento:** Folsom. **San Benito:** 5–10 mi N Idria (Gem Mine). **San Bernardino. San Diego. San Luis Obispo. Santa Barbara:** 3 mi W Cachuma Lake, Santa Cruz Island, 2 mi E Solvang. **Santa Clara:** San Antonio Valley, San Jose. **Shasta:** Redding, 3 mi S Round Mountain. **Siskiyou:** Klamath River 8 mi N Yreka, Lava Beds National Monument (S edge), Sheepy Peak (5 mi W Tulelake). **Solano:** Green Valley (W Fairfield). **Trinity:** Junction City, 13 mi SE Zenia. **Tulare:** Three Rivers. **Tuolumne. Ventura. Yolo:** Davis, Monticello Dam. COLORADO: **Arapahoe:** Littleton. **Bent:** 2 mi S Hasty, 23 mi S Las Animas. **Boulder:** Lyons Quarry, Marshall, White Rocks (5 mi E Boulder). **Jefferson:** Clear Creek. **Larimer:** Fort Collins. **Mesa:** Colorado National Monument. **Otero:** Rocky Ford. **Weld:** Nunn, Pawnee National Grassland. IDAHO: **Butte:** 6 mi S Howe. **Elmore:** 3 mi W Hammett, 13 mi S Sunnyside. **Gooding:** 3 mi S Gooding. **Owyhee.** KANSAS: **Logan, Scott, Stanton:** —. MONTANA: **Beaverhead:** 5 mi W Dillon. NEVADA: **Clark:** W Juanita Springs (10 mi S Riverside), 14 mi SW Mesquite, 7 mi NW Moapa. **Douglas:** 3 mi S Genoa, Topaz Lake. **Elko:** 7 mi E Carlin. **Esmeralda:** 15 mi S Goldfield. **Eureka:** 19 mi N Eureka. **Lincoln:** Garden Wash (ca. 12 mi E Carp). **Lyon:** Dayton. **Mineral:** 5 mi NW Schurz. **Storey:** Lagomarsino Canyon. **Washoe.** NEW MEXICO: **Bernalillo:** Albuquerque. **Guadalupe:** Santa Rosa. **Lincoln:** Rio Ruidoso in White Mts. **Otero:** Alamogordo. **Roosevelt:** Milnesand. **Socorro:** 14 mi W Magdalena. OREGON: **Jackson:** Gold Hill. **Klamath:** Klamath Falls, Sprague River Campground. **Malheur:** 50 mi W Jordan Valley. TEXAS: **Brewster:** 9 mi S Alpine. **Ector:** Odessa. **Jeff Davis:** Davis Mts., 10 mi NW Fort Davis, Musquiz Canyon near Mitre Peak. UTAH: **Box Elder:** Brigham City. **Emery:** 9 air mi E Castle Dale, 15 mi NW Woodside. **Garfield:** Capitol Reef National Park. **Grand:** Crescent Junction, Salt Valley (NW Arches National Park). **Kane:** Kanab. **Millard:** 12 mi NW Fillmore. **San Juan:** Kane Springs (E Natural Bridges National Monument). **Uintah:** SW Bonanza, Ouray Valley. **Washington:** 1 mi W Leeds, Snow Canyon. WASHINGTON: **Kittitas:** Whiskey Dick Canyon (8 mi N Vantage). WYOMING: **Converse:** Glenrock. **Niobrara:** northern part. **Platte:** —.

MEXICO: **Baja California Norte:** El Rosarito (114°W), 6 mi NE Santa Rosalillita (28°45′N, 114°10′W). **Baja California Sur:** El Pescadero, Los Angeles (Rancho), Los Barriles, 4 mi WSW Miraflores, Playa San Cristóbal. **Sinaloa:** 80 km E Mazatlán. **Sonora:** Guaymas. **Zacatecas:** 9 mi N Ojocaliente.

FIGURE 85. Geographic distribution of *Tachysphex amplus* W. Fox

Tachysphex yolo Pulawski

(Figures 86, 87)

Tachysphex yolo Pulawski, 1982:37, ♀, ♂. ! Holotype: ♂, California: Yolo Co.: Davis (UCD).—Elliott and Kurczewski 1985:294; Kurczewski 1987:119.

DIAGNOSIS.—*Tachysphex yolo* has transversely oriented midscutal setae, a horizontal depression at apex of sternum I, and a punctate mesopleuron (punctures indistinct in some individuals). Other species share this combination of characters, but the female of *yolo* has a distinctive clypeus and sternum II: the dense clypeal punctation reaches the lip base laterally (Fig. 86a, b) so that the sparsely punctate, apical area does not extend laterad to the lip corner level (its width is about 0.5–0.8 of the lip foremargin); and in most specimens there is no micropunctation along midline of sternum II from the base (or nearly so) to apex. In other species, the dense punctation of the clypeus does not reach the lip base (the sparsely punctate, apical area is as wide as the lip or nearly so), and the micropunctation of sternum II in most specimens is absent only from an apicomedian, triangular area. The male resembles *lamellatus* and *sonorensis* in having nonvelvety sternal pubescence, but unlike these species its clypeal lip (Fig. 86c–e) is not triangular. Unlike most *lamellatus*, the hypostomal carina of *yolo* is not lamelliform, and unlike the male of *sonorensis*, flagellomeres III and IV are about equal in length. Subsidiary recognition features

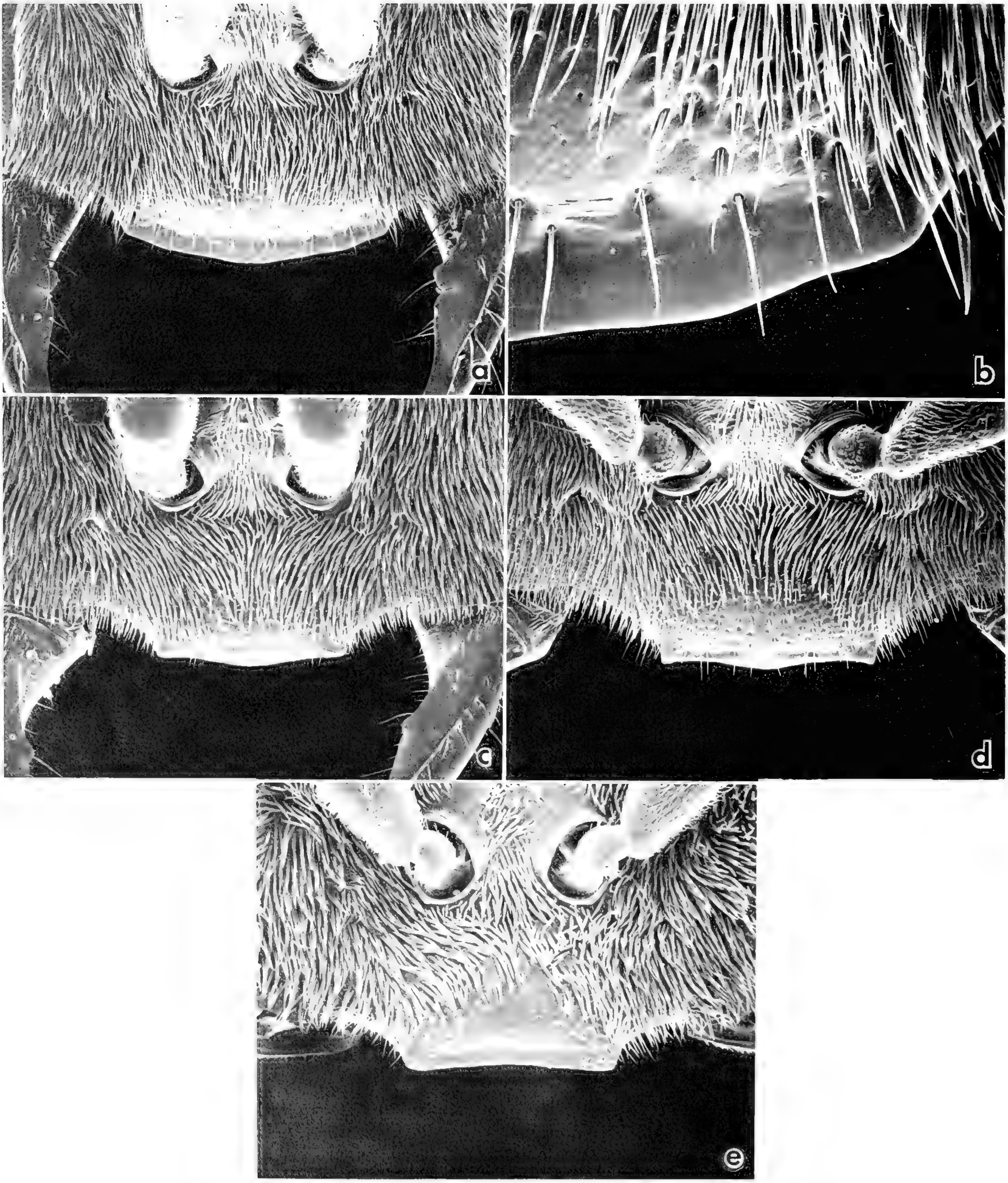

FIGURE 86. *Tachysphex volo* Pulawski. a—female clypeus, b—anterolateral portion of female clypeus, c–e—male clypeus

are: mesopleural punctures subcontiguous, ridges of propodeal side evanescent in many specimens, and foretarsal rake present in many males.

Description (see also Table 2 under *texanus,* p. 123).—Punctures subcontiguous on mesopleuron (evanescent in some specimens); up to two or three diameters apart on vertex; less than one diameter apart on scutum or (some females) a few punctures two to three diameters apart. Propodeal dorsum evenly areolate or finely rugose; side ridged but ridges evanescent in many specimens.

Setae about 1.0 MOD long on vertex; appressed or nearly so on mesopleuron except subappressed to suberect on hypoepimeral area; midscutal setae in some desert specimens forming a rosettelike pattern: setae near pronotum directed anterad.

Legs black, tarsal apex reddish, but hindfemur and hindtibia partly red in two females from Paradise Canyon, Utah (CAS, USU), and entirely red in another female from the same locality (USU), in a female from Blythe, California (UCD), and in three females from Rainbow Valley, Arizona (CAS, UAT). Gaster red or (some males from Davis, California) terga IV–VII dark brown. Terga I–IV silvery fasciate apically. Wings hyaline or nearly so.

♀.—Clypeus (Fig. 86a, b): bevel varying from markedly shorter than basomedian area to (some specimens) as long as the latter, not extending laterad to lip corner (equal to 0.5–0.8 of lip free margin); lip arcuate. Dorsal length of flagellomere I 2.0–2.4 × apical width. Vertex width : length ratio: 0.9–1.1. Discal micropunctures of tergum II one to two diameters apart. Punctation of tergum V sparse or (some specimens) dense laterally. Length 7.5–10.0 mm.

♂.—Mandibular inner margin and clypeal lip varying (see Variation below), distance between lip corners slightly more to slightly less than distance between corner and orbit. Dorsal length of flagellomere I 1.2–1.5 × apical width. Vertex width 1.3–1.5 × length. Sterna minutely, densely punctate except sternum II narrowly impunctate at apex. Outer margin of forebasitarsus with none to four preapical spines whose maximum length may attain 1.5 × width of basitarsus; outer apical spine of foretarsomere II much shorter to slightly longer than foretarsomere III. Length 5.5–6.5 mm.

Sternal pubescence not velvety, integument easily visible.

Variation.—The vestiture and male clypeus vary considerably in specimens from various localities. The greatest differences are between individuals from desert and nondesert habitats, as described below.

Vestiture. In specimens from nondesert habitats (e.g., Davis, California), the integument is not totally obscured by vestiture between the antennal socket and orbit; it is easily visible on the mesopleuron. In specimens from deserts (e.g., Borrego Valley, California), the sculpture is totally concealed between the antennal socket and orbit, and partly so on the mesopleuron. Specimens from many localities are intermediate.

Clypeal lip of male (Fig. 86c–e). It can be: (a) slightly sinuate, (b) slightly arcuate, (c) straight, or (d) with foremargin slightly concave. These conditions are not sharply delimited, and intermediates exist. Type a occurs mainly in nondesert habitats, and type d only in deserts. More than one type can be found in most localities, and all four have been collected at Lone Pine, California.

Mandible of male. The inner mandibular margin of most specimens has a widely obtuse tooth (Fig. 86c). The tooth is sharp in two males from the Providence Mountains State Park, California (CAS), in which the clypeus is of type d.

Life History.—A female of this species (UCD) was collected on flowers of *Chrysothamnus nauseosus* (Pall.) Britton at Newcomb, New Mexico. A paratype female from St. Anthony, Idaho, was collected while walking on the ground with a small nymph of *Melanoplus foedus* Scudder (Elliott and Kurczewski 1985). A female from Eureka area, Utah, is pinned with a juvenile *Melanoplus* sp. (Kurczewski 1987).

Geographic Distribution (Fig. 87).—West Coast to southern Texas, north to Oregon, south to Baja California and Sinaloa, Mexico.

Material Examined.—543♀, 662♂.

Records.—UNITED STATES: ARIZONA: **Cochise:** Bowie, Willcox (also 1 and 3.5 mi S, 2 mi E). **Coconino. Graham:** Roper Lake State Park (6 mi S Safford). S side of San Carlos reservoir. **Maricopa. Mohave. Navajo:** Jadito Trade Post. **Pima:** 18 mi W Sells, Tucson. **Pinal. Santa Cruz:** Tumacacori Mts. **Yavapai:** 8 mi N Aguila. **Yuma.** CALIFORNIA: **Alameda:** Arroyo Valle. **Colusa:** 2 mi E Colusa. **El Dorado:** Chili Bar. **Fresno:** 25 mi E Fresno, Jacalitos Canyon. **Humboldt:** Garberville. **Imperial. Inyo. Kern:** Johannesburg, Kernville. **Lake:** Northern Fork of Cache Creek at Highway 20. **Lassen:** Hallelujah Junction. **Los Angeles. Mendocino. Mono:** Benton Inspection Station, Paradise Camp. **Monterey:** Fort Ord, Monterey, Soledad. **Modoc:** Adin Pass, Fandango Pass. **Placer:** Emigrant Gap. **Plumas:** Chilcoot, Halstead Campground (E branch North Fork Feather River) **Riverside. Sacramento:** Grand Island, Sacramento, Sacramento River Levee. **San Benito:** Pinnacles National Monument. **San Bernardino. San Diego. San Joaquin:** 8 and 10 mi SW Tracy. **San Luis Obispo:** Black Lake Canyon, 10 mi W Simmler. **San Mateo:** 10 mi SW San Francisco. **Santa Barbara:** 3 mi W Cachuma Lake, Los Prietos, 2 mi E Solvang. **Santa Clara:** San Jose. **Shasta:** Old Station. **Sierra:** 6 mi E Downieville. **Siskiyou:** Dorris, Hawkinsville–Lona Gulch, Klamath River 8 mi N Eureka, Swallows (13 mi N Yreka). **Sutter:** Nicolaus. **Trinity:** Hayfork Agricultural Station, Junction City. **Tuolumne:** Hetch Hetchy Dam. **Ventura. Yolo. Yuba:** 18 mi NE Marysville. COLORADO: **Weld:** Roggen. IDAHO: **Franklin:** Preston. **Fremont:** St. Anthony Sand Dunes. **Lincoln:** 6 mi NE Shosone. NEVADA: **Churchill. Clark. Esmeralda:** 7 mi N Dyer, 15 mi W Tonopah. **Humboldt:** 10 mi N Winnemucca. **Lyon:** Weeks. **Mineral:** Luning, 3 mi SE Schurz (also 4.5 mi S). Teels Marsh Sand. **Nye:** 4 mi S Warm Springs (also 13 mi W). **Pershing:** Woolsey. **Washoe.** NEW MEXICO: **De Baca:** Sumner Lake State Park. **Dona Ana:** Las Cruces, Leesburg Dam State Park, 4 mi E Mesilla Park. **Hidalgo:** 14 mi N Animas. **Lincoln:** Devil's Canyon (20 mi NE Ruidoso), 5 mi S Oscura. **Luna:** Columbus. **Otero:** Alamogordo, White Sands National Monument. **San Juan:** Newcomb **Socorro:** 1 mi SW Bernardo Sevilletta National Wildlife Refuge, La Joya (20 mi N Socorro), 22 mi S Socorro. **Valencia:** Acoma Pueblo. OREGON: **Deschutes:** Smith Rock State Park. **Josephine:** 8 mi W Grants Pass. **Klamath:** Bonanza. **Morrow:** Boardman. **Umatilla:** Hat Rock State Park. TEXAS: **Brewster:** 2 mi E Study Butte. **Duval:** 18 mi N San Diego. **Hidalgo:** Bentsen Rio Grande Valley State Park, Santa Ana Wildlife Refuge. **Hudspeth:** McNary, Sierra Blanca. **Jim Wells:** Palito Blanco. **Presidio:** 5 mi E Presidio. **Ward:** 6 mi E Monahans. **Webb:** 9 mi SSE Laredo. UTAH: **Cache:** Cornish. **Emery. Garfield:** Bullfrog Creek area near Lake Powell. **Grand:** Crescent Junction, Moab. **Juab:** 12 mi S Eureka, White Sands Dunes (25 mi SW Eureka). **Millard:** 15 mi N Delta, Pahvant (near Flowell) **San Juan:** 6 mi S La Sal Junction. **Washington:** Leeds Canyon, Paradise Canyon **Wayne:** 8 mi N Hanksville

MEXICO: **Baja California Norte:** 4 mi N Bahía de los Angeles, 10 mi E Bahía San Quintin, Cataviña, 9 mi SW Colonet, Descanso, El Crucero, El Portezuelo (39 road mi S Cataviña), 25 km SE Laguna Chapala, 20 mi N Mesquital, El Progreso (Sierra Juárez), 3 mi NE Mission San Borja, 38 km S Rosarito (114°W), 3 mi N San Felipe, San Quintin (also 10 and 40 mi S), San Vicente, 1–3 mi SE Santa Rosalillita (28°44′N, 114°08′W). **Baja California Sur:** 12 mi E Bahía Tortugas, Desierto Vizcaíno (27°35′N, 114°10′W), 28 mi SW El Crucero, El Pescadero, 7 and 9.2 mi SE Guerrero Negro, 12 mi S Guillermo Prieto, Laguna Ojo de Lievre (27°46′N, 114°10′W), La Paz, 13 air km WNW La Purisima, Los Barriles, Los Frailes, 16 mi E Rosarito, San Carlos, 15 mi N San Ignacio, E edge of Sierra Placeres (27°35′N, 114°30′W). **Chihuahua:** Moctezuma, Samalayuca. **Sinaloa:** 8 mi S Elota. **Sonora:** Cerro Pinacate (McDougal Crater), Guaymas, 39 mi S Puerto Peñasco, Tepoca Bay

FIGURE 87 Geographic distribution of *Tachysphex yolo* Pulawski

Tachysphex yuma Pulawski

(Figures 88, 89)

Tachysphex yuma Pulawski, 1982:39, ♀, ♂. ! Holotype: ♂, Mexico: Baja California Sur: La Paz (CAS, Type #13966)

DIAGNOSIS.—*Tachysphex yuma* has a punctate mesopleuron (punctures shallow), the midscutal setae are oriented posterolaterad (transversely in some males), and sternum I has an apical depression (which is weakly defined in some specimens). Several other species share this combination of characters, but they have a uniformly ridged propodeal side (ridges evanescent in many *yolo*). In *yuma*, the propodeal side varies: it is either coarsely ridged posteriorly and microridged along the metapleural sulcus; or (most specimens) nonridged along the metapleural sulcus and ridged along the dorsal margin (Fig. 88b), or dorsal and posterior; or all unridged (some males). Furthermore, the flagellum of *yuma* is somewhat longer; for example, the length of flagellomere IV is 3.6–4.2 (female) and 2.0–2.4× (male) width, and up to 3.2 and 2.0×, respectively, in the other species. In the male, the unusually broad clypeal lobe is distinctive (see Description below), and the velvety sternal pubescence is an additional recognition feature.

DESCRIPTION (see also Table 2 under *texanus*, p. 123).—Punctures nearly contiguous or some punctures up to two diameters apart on vertex; nearly contiguous on scutum or (some specimens) one to several diameters apart on disk; shallow on mesopleuron, averaging less than one to more than one diameter apart beneath mesopleural scrobe. Propodeal dorsum evenly microareolate to slightly rugose; side in most specimens ridged along dorsal and often posterior margins, unridged along metapleural sulcus (Fig. 88b); unridged in some males; entirely ridged in a female from Redding, California, but ridges evanescent anteriorly and coarse posteriorly.

Setae 1.0 MOD long on vertex; on scutum at middle oriented mostly posterolaterad, but transversely in some males; erect or nearly so on hypoepimeral area; subappressed below mesopleural scrobe.

Mandible in most specimens reddish at middle; gaster red or (single male from Todos Santos, Mexico) tergum I black. Legs usually black, with tarsal apex reddish, but largely red in a female from Deep Canyon, California (are red: forefemur apically, midfemur apically and ventrally, hindfemur, tibiae partly, tarsi). Terga I–IV silvery fasciate apically (fasciae interrupted in female); only hindfemur and tarsal apex are red in a female from Chocolate Mountains, California. Wings moderately infumate to (many males) hyaline.

♀.—Clypeus (Fig. 88a): bevel about as long as basomedian area; lip arcuate. Dorsal length of flagellomere I 2.4–3.0× apical width; of flagellomere IV 3.6–4.2× width. Vertex width 1.0–1.2× length. Dorsal micropunctures of tergum II two to three diameters apart. Tergum V sparsely punctate at middle. Length 10.5–12.0 mm.

Vestiture not obscuring sculpture between antennal socket and orbit. Scutal setae mostly appressed, but some setae erect, about 0.5 MOD long.

♂.—Clypeus (Fig. 88c): bevel ill defined; lip straight or with obtuse, median projection, its corners well defined; distance between corners 1.4–1.6× clypeal length and 1.4–1.5× the distance between corner and orbit. Dorsal length of flagellomere I

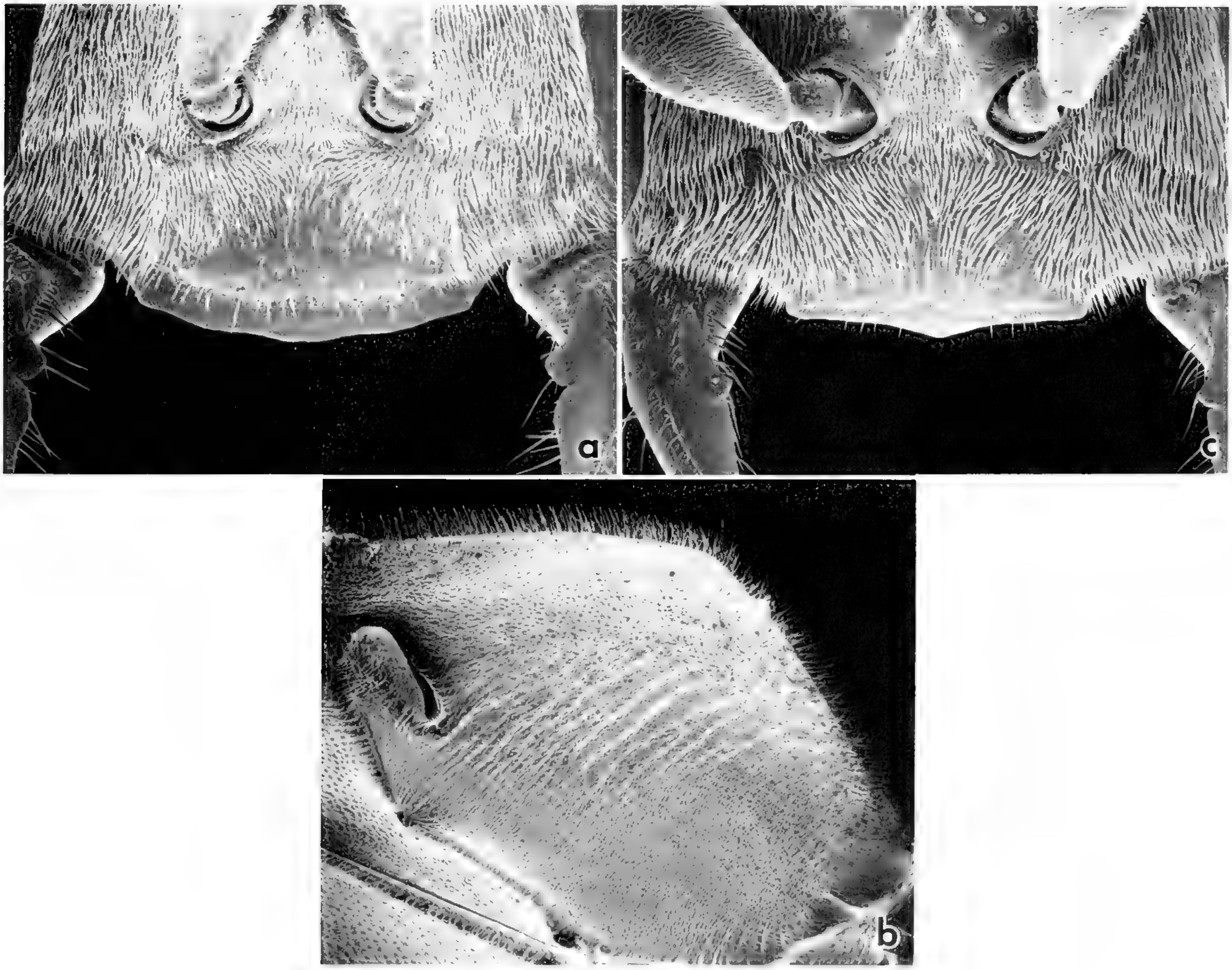

FIGURE 88. *Tachysphex yuma* Pulawski: a—female clypeus; b—female propodeum; c—male clypeus

1.4–1.7× apical width; of flagellomere IV 2.0–2.4× width. Vertex width 1.2–1.7× length. Sterna evenly, minutely punctate (punctures less than one diameter apart), but sterna II–V apically impunctate, glabrous. Outer margin of forebasitarsus without preapical spines or (occasional specimens) with one or two such spines that are shorter than basitarsal width. Length 7–11 mm.

Integument largely obscured by vestiture between antennal socket and orbit. Scutal setae suberect, about 0.5 MOD long. Sternal pubescence velvety, largely obscuring integument.

GEOGRAPHIC DISTRIBUTION (Fig. 89).—Idaho, Oregon, California, southern Nevada, Arizona, southwestern Texas, northern Mexico (Sonora, Baja California).

MATERIAL EXAMINED.—44♀, 63♂ (CAS, CIS, CSDA, CSU, CU, KU, LACM, NSCA, NYSU, SDNH, UAE, UCD, UCR, UIM, UMMZ, USNM, USU)

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** Portal (also 5 and 6 mi SW). **Coconino:** Grand Canyon National Park (15 mi NE Phantom Ranch). **Maricopa:** Wickenburg. **Santa Cruz:** Canelo. **Yavapai:** Yarnell. CALIFORNIA: **Imperial:** Black Mountain (Chocolate Mts.), 20 mi E Glamis. **Inyo:** Bishop, Darwin Falls, Panamint Springs, Surprise Canyon. **Los Angeles:** Claremont. **Riverside:** Boyd Desert Research Center (4 mi S Palm Desert), Deep Canyon, Palm Springs, Salton Beach, Thousand Palms Canyon, Whitewater. **San Bernardino:** 3 mi N Cross Roads. **Shasta:** Redding. **Stanislaus:** Empire. **Tuolumne:** Mather. IDAHO: **Twin Falls:** Rock Creek Canyon (19 mi S Hansen). NEVADA: **Clark:** Juanita Springs (10 mi S Riverside). OREGON: **Malheur:** 4 mi N Juntura. TEXAS: **Brewster:** 20 mi NNW Marathon

MEXICO: **Baja California Norte:** 30 mi N Guerrero Negro, Isla de Cedros (Punta Norte, Cerro de Cedros), 65 mi S San Felipe. **Baja California Sur:** 30 mi ESE Bahía Tortugas, 35 km S Mulege, Rancho El Coyote, 16 mi E Rosarito, 3 and 15 mi W San Ignacio (also 10 mi E), Todos Santos. **Sonora:** Bahia San Carlos

Tachysphex texanus (Cresson)

(Figures 90–92)

Larrada texana Cresson, 1872:214, ♀, ♂. ! Lectotype: ♀, Texas: no specific locality (ANSP), designated by Cresson 1916:96.—In *Tachytes*: Patton 1879:368, Snow 1881:99.—In *Larra*: Patton 1881:389, Kohl 1885:248.—In *Tachysphex*: W. Fox 1894*a*:513; Dalla Torre 1897:686, Ashmead 1899:250, Hartman 1905:29, Williams 1914:166, 206, Mickel 1918:422, G. Bohart 1951:953, Krombein 1967:394; Bohart and Menke 1976:277; Krombein 1979:1630; Rust et al. 1985:46, 53; Kurczewski 1987:122

Tachysphex sepulcralis Williams, 1914:169, ♀, ♂. ! Holotype: ♀, Kansas: Phillips

FIGURE 89. Geographic distribution of *Tachysphex yuma* Pulawski.

Co: no specific locality (KU). Synonymized by Pulawski *in* Krombein 1979:1630.—Krombein 1953*a*:330, LaBerge 1956:528 (as *sepulchralis*); Krombein 1958*c*:188, 1967:393, Arnaud 1970:33, Bohart and Menke 1976:277.

Tachysphex mancei Banks, 1921:19, ♀, ♂. Holotype: ♂, North Carolina: Southern Pines (MCZ). Synonymized with *sepulcralis* by G. Bohart 1951:952.—Brimley 1938:443.

DIAGNOSIS.—*Tachysphex texanus,* a common transcontinental species, belongs to a lineage within the *pompiliformis* group in which midscutal setae are oriented laterad (Fig. 90b, c), mesopleural punctures are well defined (Fig. 91a, b), and sternum I has a horizontal depression at apex (Fig. 91c, d). No one character separates the female from all other species of the lineage, but the following combination is diagnostic: (1) mesopleural setae appressed or nearly so below scrobe (subappressed to suberect below the scrobe in *sonorensis* and *tsil*), (2) punctures average less than one diameter apart below mesopleural scrobe (more than one diameter in *sonorensis, tsil,* and many *lamellatus*), (3) mesopleural integument easily visible (partly obscured by vestiture in many *yolo*), (4) clypeal lip arcuate (sinuate in *huchiti,* undulate in *arizonac* and *lamellatus*), (5) dense punctation of clypeal lobe not attaining lip base (attaining lip base laterally in *yolo*), (6) dorsal length of flagellomere I 1.9–2.2× apical width in eastern and 2.0–2.4× in western populations (2.0–2.1× in *huchiti,* a western species), (7) length of flagellomere IV no more than 3.2× width (3.6–4.2× in *yuma*), (8) propodeal side evenly ridged (ridges evanescent in many *yolo,* absent anteriorly in *yuma*), (9) sternum II micropunctate basally and laterally (micropunctures absent from base to apex along midline in most *yolo*), and (10) body length 7.5–10.5 mm (6.5–9.0 mm in *huchiti*).

The male of *texanus* differs from most of these species in having a basically truncate (Fig. 90d, e) clypeal lobe (instead of triangular) and also in having velvety sternal pubescence (Fig. 91e). *Tachysphex arizonac* is similar, but in that species the corner of the clypeal lobe is more prominent (Fig. 95b), and the mesopleural setae are suberect below the scrobe (setae appressed or nearly so in *texanus*). *Tachysphex yuma* and *tsil* also are similar, but in the former the clypeal lobe is much broader, and in the latter it is much narrower, than in *texanus* (compare Fig. 90d and 99).

DESCRIPTION (see also Table 2).—Punctures up to one or two diameters apart on vertex; less than one diameter apart on scutum in most specimens (a few discal punctures sometimes more than that); averaging less than one diameter apart beneath mesopleural scrobe (but more than that in some males), subcontiguous in most females. Propodeal dorsum usually rugose, occasionally areolate. Discal micropunctures of tergum II two to three diameters apart.

Vestiture dense but not entirely obscuring integument between antennal socket and orbit. Setae 0.8–1.0 MOD long on vertex, appressed beneath mesopleural scrobe.

Legs black, tarsal apex brown. Gaster red to black (see Variation below), terga I–III or I–IV silvery fasciate apically. Wings hyaline to slightly infumate.

♀.—Clypeus (Fig. 90a): bevel equal to basomedian area or shorter; lip arcuate, slightly obtusely projecting mesally in some specimens. Dorsal length of flagellomere I 1.9–2.4× apical width. Vertex width slightly more to slightly less than length. Tergum V densely punctate (except in some females from California and Mexico). Length 7.5–10.5 mm.

Scutal setae appressed, but usually a few sparse, suberect setae present, about as long as 0.6 MOD.

♂.—Clypeus (Fig. 90b, c): bevel delimited laterally by short,

TABLE 2. SOME CHARACTERS OF *TACHYSPHEX TEXANUS* AND ITS RELATIVES.

Character	Species								
	am	ar	hu	la	so	te	ts	yo	yu
Frontal punctures									
Less than one diameter apart in all individuals	1	1	1	1	0	1	1	1	1
Up to one diameter apart in some females	0	0	0	0	1	0	0	0	0
Mesopleural punctures									
Well-defined in all individuals	1	1	1	1	1	1	1	0	1
Evanescent in some individuals	0	0	0	0	0	0	0	1	0
Propodial side ridges									
Present in all individuals	1	1	1	0	1	1	1	0	0
Evanescent in some individuals	0	0	0	1	0	0	0	1	1
Propodeal hindface ridged	1	1	1	1	1	1	1	1	1
Sternum I apicomesally									
With horizontal depression	0	1	1	1	1	1	1	1	1
Gradually sloping	1	0	0	0	0	0	0	0	0
Hindcoxa									
Carinate on whole length	0	1	0	0	1	1	1	1	1
Carinate basally	0	0	1	1	0	0	0	0	0
Finely ridged along inner margin	1	0	0	0	0	0	0	0	0
Vertex setae erect	1	1	1	1	1	1	1	1	1
Midscutal setae oriented									
Laterad in all individuals	1	1	1	1	0	1	0	0	0
Laterad or posterolaterad	0	0	0	0	1	0	1	0	1
Laterad or radially	0	0	0	0	0	0	0	1	0
Setae of propodeal dorsum oriented anterolaterad	1	1	1	1	1	1	1	1	1
Setae of midfemoral venter appressed or nearly so	1	1	1	1	1	1	1	1	1
Head and thorax black	1	1	1	1	1	1	1	1	1
Frontal vestiture									
Silvery in all individuals	0	1	1	1	1	1	1	1	1
With golden tinge in some males	1	0	0	0	0	0	0	0	0
Female clypeal lip									
Notched mesally	0	0	0	0	0	0	0	0	0
Incised laterally	0	0	0	0	0	0	0	0	0
Female: apical depression of tergum V punctate	0	0	0	0	0	0	0	0	0
Female: pygidial plate alutaceous, punctate	1	1	1	1	1	1	1	1	1
Female: trochanteral venter minutely, densely punctate	1	1	1	1	1	1	1	1	1
Male: mandibular inner margin.									
With tooth in all specimens	1	1	0	0	0	1	1	0	1
With tooth in some specimens	0	0	0	0	0	0	0	1	0
Without tooth	0	0	1	1	1	0	0	0	0
Male clypeal bevel in relation to basomedian area:									
Shorter to equal in length	1	0	0	0	0	0	0	0	0
Shorter	0	1	1	1	1	1	1	1	1
Male: sternal pubescence velvety	1	1	1	0	0	1	1	0	1
Male forefemoral notch									
Pruinose in all individuals	1	1	1	1	0	0	1	1	1
Glabrous in some individuals	0	0	0	0	1	1	0	0	0
Male: preapical spines on outer margin of foretarsus:									
Present in all individuals	0	0	0	0	1	0	0	0	0
Present in some individuals	0	0	0	0	0	0	0	1	1
Male: outer apical spine of foretarsomere II in relation to foretarsomere III:									
Shorter in all individuals	1	1	1	1	1	1	1	0	1
Longer in some individuals	0	0	0	0	0	0	0	1	0

0 = character absent, 1 = character present, am = *amplus*, ar = *arizonae*, hu = *huchiti*, la = *lamellatus*, so = *sonorensis*, te = *texanus*, ts = *tsil*, yo = *yolo*, yu = *yuma*

small, longitudinal carina extending from lip corner; lip straight, arcuate or sinuate, with prominent corners that are about as close to orbit as to each other (in most specimens from Baja California, the distance between corners is about 0.8 of distance between a corner and orbit). Dorsal length of flagellomere I 1.1–1.4 × apical width. Vertex width 1.2–1.4 × length. Sterna evenly, minutely punctate (punctures less than one diameter apart), but sterna II–V apically impunctate, glabrous. Length 6–8 mm.

Scutal setae suberect, 0.8–1.0 MOD long. Sternal pubescence velvety.

VARIATION.—*Tachysphex texanus*, a widely distributed species, varies geographically in the color of the gaster and in the form of the male clypeus. Several forms can be distinguished, but I do not recognize them as formal subspecies because of intergradation in broad intermediate areas.

1) Generally, the gaster is black in specimens taken east of

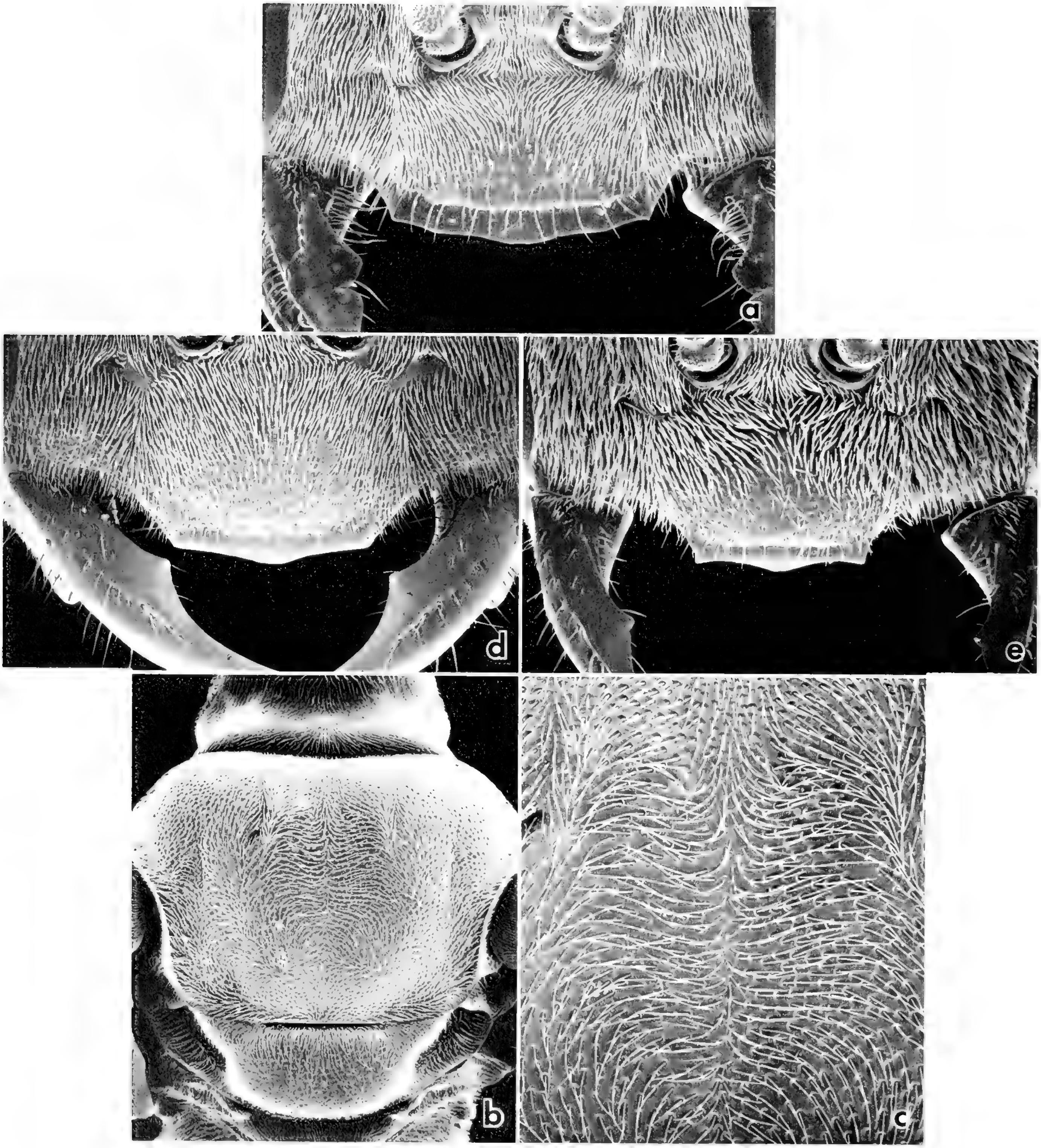

FIGURE 90. *Tachysphex texanus* (Cresson): a—female clypeus; b—female pro- and mesothorax, dorsal view, c—midscutal setae of female; d—male clypeus; e—same, different specimen

the 95th meridian, as well as many Kansas individuals. The length of female flagellomere I is 1.9–2.2 × width, and the clypeal lip of most males is sinuate (with a mesal projection) or arcuate.

2) Specimens from Nebraska, South Carolina, Georgia, Alabama, and Florida are similar to the previous form, but gastral segments I–III are red. However, one male from Gainesville, Florida, is all black.

3) West of the 95th meridian (except many Kansas specimens) the gaster is red, although segments V–VII may be brown in occasional males. The length of female flagellomere I is 2.0–

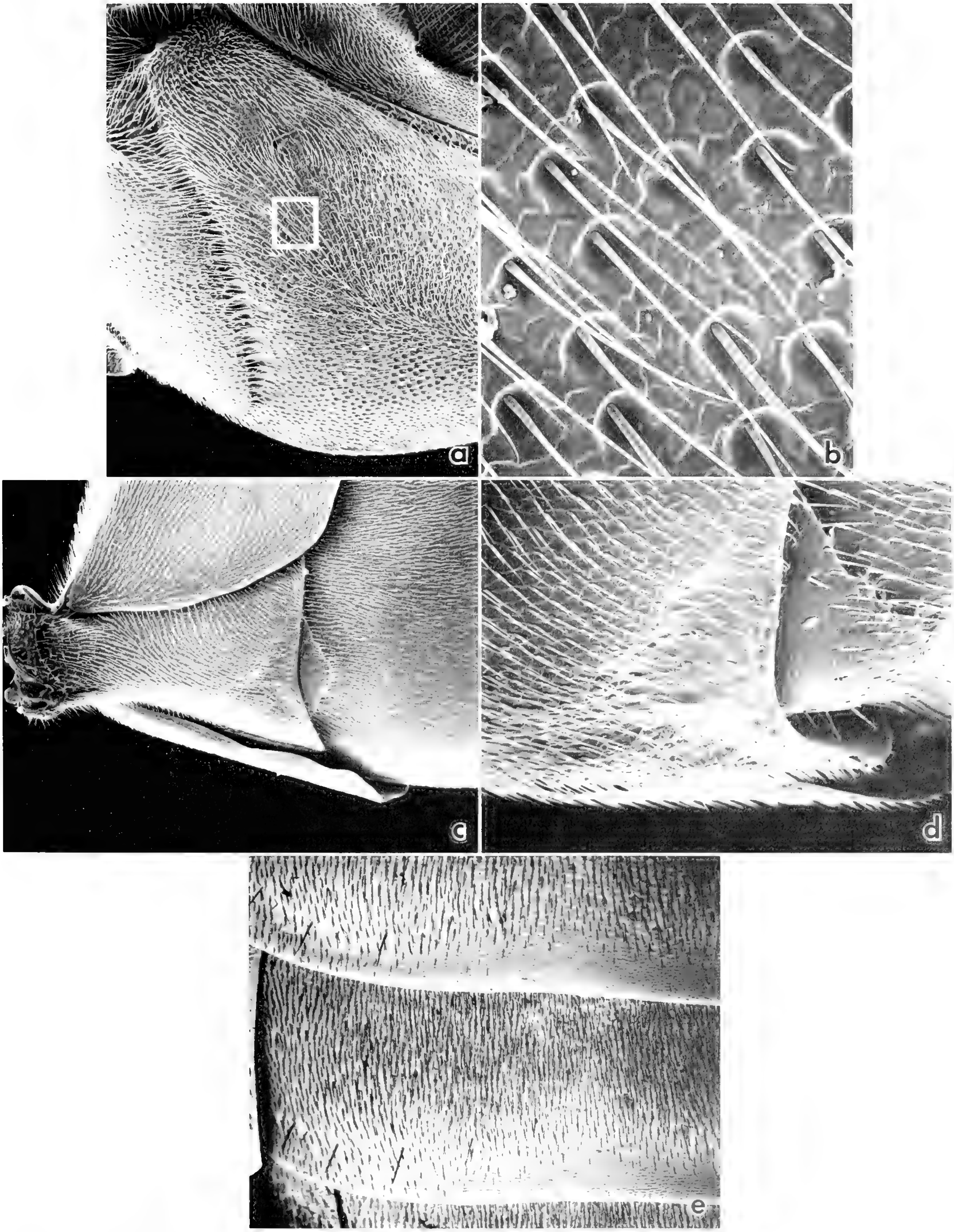

FIGURE 91. *Tachysphex texanus* (Cresson): a—female mesopleuron, b—sculpture of female mesopleuron, c—base of gaster, oblique view, d—apex of sternum I and base of sternum II, oblique view; e—apex of male sternum II and sternum III.

2.4× width, and the clypeal lip of most males is straight or nearly so, or it has a small, mesal projection; it may also be sinuate.

The velvety pubescence of the male sterna normally is so dense that it almost totally obscures the integument. However, it is relatively sparse in three males from Glenrock, Wyoming (USNM), in which the integument is easily visible.

Life History.—Krombein (1953*a*) observed *texanus* on the foliage of *Pinus serotina* Michx. and *Liquidambar*. A male (UMMZ) from E. S. George Reserve, Michigan, was collected on flowers of *Daucus carota* L., and two females (CIS) from Animas, New Mexico, were taken on flowers of *Helianthus annuus* L. Williams (1914) observed a female carrying her prey, an immature oedipodine grasshopper of very small size that Kurczewski (1987) identified as *Arphia* sp. Rust et al. (1985) noted a female collected with its acridid prey, an immature *Encoptolophus robustus* Rehn and Hebard, on Santa Cruz Island, California. Kurczewski (1987) observed a nesting female near Lecompton, Kansas. Prey were flow to the nest and either taken inside directly or first dropped at the entrance and then pulled in. Kurczewski did not say it explicitly, but his observation suggests that the nest was permanently open during the provisioning period. The nest had an oblique gallery and a single, fully provisioned cell that contained four acridid prey. Three prey were nymphal *Melanoplus* sp. near *flavidus* Scudder and one was a nymphal *Orphulella pelidna* (Burmeister). The egg was laid on the forecoxal corium of the second largest prey, and extended between the fore- and midcoxae. Hartman (1905) reported that *texanus* caught and impaled a fly "of the domestic species," but this statement indicates that he was observing an *Oxybelus*.

Geographic Distribution (Fig. 92).—Alberta to central Mexico; transcontinental.

Material Examined.—980♀, 1,004♂.

Records (b: gaster all or predominantly black).—CANADA: **Alberta:** 10 mi N Coaldale, Writing-on-Stone Provincial Park.

UNITED STATES: ALABAMA: **Baldwin:** Gulf Shores. **Montgomery:** Montgomery. ARIZONA: **Apache:** 5 and 10 mi W Springerville, Vernon. **Cochise. Coconino:** Antelope Hills (25 mi N Flagstaff). **Maricopa:** 3 mi SW Maricopa, Wickenburg (also 5 mi SE). **Mohave:** 3 mi E Hackberry, Wikieup. **Navajo:** 10 mi N Show Low. **Pima. Pinal:** Picacho Pass. **Santa Cruz. Yavapai:** Congress, Yarnell in Weaver Mts. ARKANSAS: **Conway:** —(b). CALIFORNIA: **Alameda. Amador:** —. **Butte:** Chico. **Contra Costa. El Dorado:** 6–9 mi NE on Icehouse road, Placerville. **Fresno. Glenn:** Artois. **Humboldt:** 3 mi NE Alderpoint, 5 mi NE Briceland, 5 mi NW Garberville. **Imperial:** Experimental Farm, Palo Verde. **Inyo. Kern. Lake:** North Fork Cache Creek at Highway 20. **Lassen:** Doyle, Hallelujah Junction. **Los Angeles:** including San Clemente Island and Santa Catalina Island. **Marin. Mariposa:** El Portal, Mariposa. **Mendocino. Merced:** Merced Falls. **Modoc:** 5 and 9 mi NE Alturas, Davis Creek. **Mono:** Aurora Canyon (4 mi E Bridgeport), Topaz Lake. **Monterey. Napa. Nevada:** Boca, 2 mi S Grass Valley, Nevada City. **Orange. Placer:** Auburn. **Plumas. Riverside. Sacramento:** Fair Oaks, Folsom (also 10 mi NE). **San Benito:** Idria, Panoche, Pinnacles National Monument. **San Bernardino. San Diego. San Francisco:** San Francisco (Lone Mountain). **San Joaquin:** Corral Hollow (8 mi SW Tracy), Tracy. **San Luis Obispo:** 5 mi S Creston, La Panza (12 mi NE Pozo), Montana de Oro State Park (3 mi SW Los Osos), Paso Robles. **San Mateo:** Menlo Park, Redwood City. **Santa Barbara:** including Santa Cruz Island and Santa Rosa Island. **Santa Clara. Santa Cruz:** 4 mi E Boulder Creek. **Shasta. Sierra:** 6 mi E Downieville, Sierraville. **Siskiyou. Solano:** Green Valley, Pleasant Valley Road 0.5 mi S Highway 128, 2 mi SE Vallejo. **Sonoma:** Cloverdale, 2 mi W Forestville, Petaluma. **Stanislaus:** Del Puerto Canyon (21 mi W Patterson). **Trinity:** Hayfork, Scott Mt. **Tulare:** Lemon Cove, Potwisha (junction of Marble and Middle Forks of Kaweah River). **Tuolumne. Ventura. Yolo.** COLORADO: **Bent:** 2 mi S Hasty. **Boulder:** Boulder. **Cheyenne:** Aroya. **Larimer:** Fort Collins. **Logan:** 10 mi E Sterling. **Mesa:** Colorado National Monument. **Otero:** La Junta. **Prowers:** Carlton. **Weld:** Owl Creek (8, 11, and 19 mi NE Nunn), 1 mi NE Roggen. CONNECTICUT: **Hartford:** Hartford (b). FLORIDA: **Alachua:** Gainesville (partly b), Monteoca (11 mi NW Gainesville). **Collier:** —. **Dade:** Fuch's Hammock near Homestead. **Gadsden:** Quincy. **Highlands:** Highlands Hammock State Park, Lake Placid, Sebring area. **Lee:** Olga. **Levy:** Cedar Key. **Liberty:** Torreya State Park. **Marion:** Lake Eaton, 9 mi SSW Ocala. **Monroe:** Big Pine Key, Fleming Key, Grassy Key. **Pinellas:** Tarpan Springs. **Polk:** Avon Park Airforce Range. **Putnam:** 2 mi NW Orange Springs. **Santa Rosa:** 4 mi W Lake Carr. **Sarasota:** Myakka River State Park. **Suwannee:** Suwannee River State Park. GEORGIA: **Clarke:** Athens. **Fulton:** Atlanta. **Liberty:** St. Catherine's Island. **Miller:** Spring Creek. IDAHO: **Ada:** Regina (also 12 mi N, 12 mi NW). **Blaine:** 2 mi W Carey. **Canyon:** Murphy. **Elmore:** 4 mi E Orchard. **Gooding:** 1 mi NE Gooding (also 12 mi N). **Nez Perce:** Lewiston. **Oneida:** Black Pine Canyon, 5 mi NW Holbrook. **Owyhee:** Silver City. **Twin Falls:** Rogerson. ILLINOIS: **Macoupin:** Carlinville (b). **Washington:** Dubois (b). KANSAS: **Barber:** 15 mi W Medicine Lodge. **Barton:** —(partly b). **Dickinson:** Abilene (b). **Douglas:** Baldwin (b), Lawrence (b). **Ellis, Graham, Grant** (b), **Hamilton, Meade, Ness, Norton, Phillips** (partly b), **Rooks, Russell** (b), **Sedgwick** (b), **Smith, Stevens:** —. MASSACHUSETTS (b): **Middlesex:** Holliston. **Norfolk:** Wellesley. MICHIGAN (b): **Iosco:** —. **Livingston:** E. S. George Reserve. **Midland, Ogemaw, Roscommon:** —. **Washtenaw:** Stinchfield Woods. MINNESOTA: **Wabasha:** 3 mi SE Dumfries (b). MISSOURI: **Boone:** Columbia (b). MONTANA: **Garfield:** 5 mi W Jordan. **Yellowstone:** 6 mi NE Pompeys Pillar. NEBRASKA: **Dawes:** Chadron. **Keith:** Ogallala. **Sioux:** 7 and 18 mi N Harrison. NEVADA: **Churchill:** Fallon, 3 mi W Hazen. **Clark. Douglas:** Topaz Lake. **Elko:** 3 mi N Currie, 50 mi S Wells. **Esmeralda:** 15 mi S Goldfield. **Eureka:** 6 mi S Beowawe, 1 mi W Emigrant Pass. **Humboldt:** Orovada. **Lander:** 2 mi NW Tenabo. **Lincoln:** 18 mi S Caliente. **Lyon:** Yerington. **Mineral:** 3 mi SE Schurz (also 4.5 mi S). **Nye:** Black Rock Summit, 24 mi E Tonopah. **Pershing:** 7 mi E Oreana. **Storey:** Lagomarsino Canyon. **Washoe.** NEW MEXICO: **Bernalillo:** Chilili. **Catron:** Pie Town. **Chaves:** Mescalero Sands. **De Baca:** Sumner Lake State Park. **Dona Ana:** Hatch, Las Cruces. **Eddy:** Carlsbad, Hope, Whites City. **Grant:** 1 mi S Silver City. **Harding:** Chicosa Lake State Park. **Hidalgo. Lincoln:** Carrizozo, Nogal. **Luna:** Columbus. **McKinley:** Pinedale. **Otero:** Alamogordo, High Rolls Mountain Park (also 3 mi W). **Quay:** Tucumcari. **San Miguel:** Las Vegas. **Santa Fe:** 10 mi N Santa Fe. **Socorro:** La Joya (20 mi N Socorro), 31 mi E San Antonio. **Taos, Torrance:** —. NEW YORK (b): **Suffolk:** Orient, Riverhead. NORTH CAROLINA: **Cumberland:** Fort Bragg (partly b). **Dare:** Kill Devil Hills (b). **Moore:** Southern Pines (b). NORTH DAKOTA: **Golden Valley:** Beach. **Ransom:** 7 mi SE Sheldon (b). OKLAHOMA: **Cimarron:** Black Mesa State Park. **Garfield, Texas:** —. OREGON: **Baker:** Pleasant Valley. **Benton:** Corvallis. **Deschutes:** Smith Rock State Park, 3 mi N Terrebonne. **Jackson:** 6 mi N Copper, Shady Cove. **Jefferson:** 10 mi S Madras. **Josephine:** Illinois Valley. **Klamath:** 3 mi S Beatty, Harpold Dam, Upper Klamath Lake. **Malheur:** 57 mi W Jordan Valley, 4 mi E Juntura. **Wallowa:** 18 mi NNE Imnaha. SOUTH CAROLINA: **Aiken:** New Ellenton. **Charleston:** McClellanville. **Horry:** Myrtle Beach. **Pickens:** Dovenhaven (7 mi NE Pickens). SOUTH DAKOTA: **Fall River:** 5 mi S Oelrichs. TEXAS: **Bastrop:** 6 mi E Bastrop (partly b). **Bexar:** Fort Sam Houston. **Bosque:** —. **Brewster. Caldwell:** Luling (b). **Crockett:** Fort Lancaster State Historical Park. **Culberson:** Kent. **Dallam:** Conlen, Dalhart. **Galveston:** Galveston (also 7 mi W). **Gillespie:** Cherry Springs. **Gonzales:** Palmetto State Park (b). **Hartley:** Weatherford Ranch. **Hidalgo:** Bentsen Rio Grande Valley State Park, McAllen Botanical Garden. **Hudspeth:** McNary, Sierra Blanca (also 5 mi E). **Jeff Davis:** Davis Mts., 10 mi W Fort Davis (also 25 mi N). **Kimble:** Junction. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **La Salle:** Cotulla. **Lee:** Fedor (partly b). **Palo Pinto:** Possum Kingdom State Park. **Presidio:** 11 mi N Presidio. **Randall:** Canyon. **Starr:** Falcon State Park. **Ward:** 1 mi S Grandfalls. **Zapata:** Falcon State Park. UTAH: **Box Elder:** 10 mi SW Snowville. **Duchesne:** Duchesne. **Emery, Garfield, Grand, Juab:** Trout Creek. **Millard:** Oak City. **Uintah:** 17 mi S Bonanza, Green River Valley. **Utah:** Lehi. **Washington.** VIRGINIA: **Prince Edward:** Farmville (b). WASHINGTON: **Grant:** Columbia River near Vantage, O'Sullivan Dam. WYOMING: **Converse:** Glenrock. **Lincoln:** Opal. **Natrona:** Powder River. **Sheridan:** 5 mi N Sheridan. **Washakie:** 11 mi SW Worland. **Weston:** Newcastle.

MEXICO: **Baja California Norte. Baja California Sur:** including Isla Cerralvo (Ruffo Ranch) and Isla San Esteban. **Chihuahua:** 10 mi N Chihuahua (also 35 and 45 mi), Hidalgo del Parral, Santa Clara Canyon (5 mi W Parrita). **Coahuila:** 15 mi N Saltillo. **Jalisco:** Lagos de Moreno. **Sinaloa:** 8 mi SE Elota, Playa Baviri (17 mi W Los Mochis). **Sonora:** Ciudad Obregón, La Playa area, San Carlos (also 6 km NNW), San Vicente. **Tamaulipas:** 30 mi S Matamoros. **Zacatecas:** 8 mi N Ojo Caliente, San Juan Capistrano (22°38′N, 104°05′W).

Tachysphex huchiti sp. n.

(Figures 93, 94)

Derivation of Name.—Named after the Huchiti Indians of southern Baja California Sur, where the holotype was collected; noun in apposition.

FIGURE 92. Geographic distribution of *Tachysphex texanus* (Cresson).

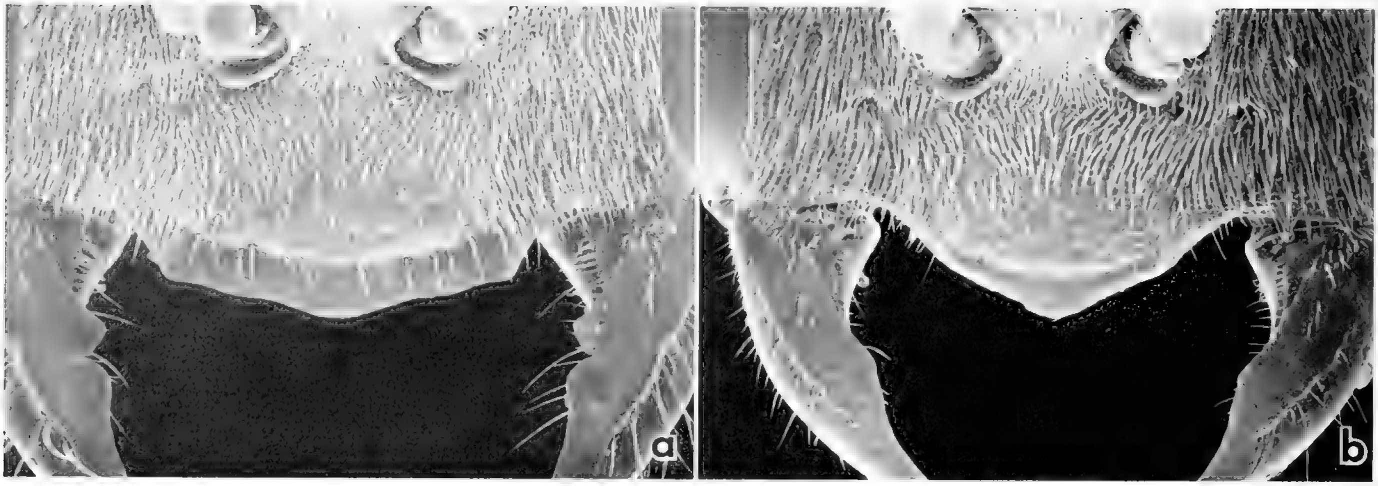

FIGURE 93. *Tachysphex huchiti* sp. n.: a—female clypeus; b—male clypeus.

DIAGNOSIS.—*Tachysphex huchiti* belongs to a lineage of the *pompiliformis* group in which the midscutal setae are directed laterad, the mesopleuron is punctate, and sternum I is apically depressed. Within this lineage, most species have conspicuous diagnostic characters allowing immediate recognition. Females of *huchiti* and *texanus* lack such characters, but the following combination separates them from the remaining species: (1) clypeal lip not undulate (undulate in *arizonae* and *lamellatus*), (2) dense punctation of clypeal lobe attaining lip corner but not lip base (attaining lip base laterally in *yolo*), (3) length of flagellomere IV no more than 3.2× width (3.6–4.2× in *yuma*), (4) punctures below mesopleural scrobe averaging less than one diameter apart (more than one diameter apart in *sonorensis, tsil,* and many *lamellatus*), (5) mesopleural setae appressed or nearly so beneath scrobe (nearly erect in many *sonorensis* and *tsil*), (6) mesopleural integument easily visible (partly obscured by vestiture in many *yolo*), and (7) propodeal side evenly ridged (ridges evanescent in many *yolo,* absent anteriorly in *yuma,* Fig. 88b). The differences between *huchiti* and *texanus* are subtle. In *huchiti,* the clypeal lip is sinuate (Fig. 93a), flagellomere I is slightly shorter (dorsal length 1.9–2.1× apical width), and average size is smaller (6.5–9.0 mm). In *texanus,* the clypeal lip is arcuate (Fig. 90a), flagellomere I is longer (dorsal length 1.9–2.2× apical width in eastern and 2.2–2.4× in western populations), and average size is larger (7.5–10.5 mm).

The male of *huchiti* can be easily recognized by the combination of an obtusely triangular clypeal lip (Fig. 93b) and velvety sternal pubescence. The nondentate inner mandibular margin is a subsidiary diagnostic character. Males of *lamellatus* are similar, but in that species the scutal setae are suberect, 1.3 MOD long anteriorly (subappressed, shorter than MOD in *huchiti*), the sternal pubescence is inconspicuous, and the hypostomal area of most specimens is distinctive (see *lamellatus* for details).

DESCRIPTION (see also Table 2 under *texanus,* p. 123).—Punctures almost contiguous on vertex and scutum, less than one diameter apart on mesopleuron. Propodeal dorsum areolate.

Vestiture obscuring integument between antennal socket and orbit from most angles. Setae about 0.8 MOD long on vertex, suberect on hypoepimeral area, appressed below mesopleural scrobe.

Legs black, tarsal apex reddish in most specimens. Gaster red (most specimens) or all black (a male from Drumheller, Alberta, and another from Surprise Canyon, California). Wings almost hyaline. Terga I–III (I–IV in many males) silvery fasciate apically.

♀.—Clypeus (Fig. 93a): bevel about as long as basomedian area; lip obtusely prominent mesally, weakly sinuate. Dorsal length of flagellomere I 1.9–2.1× apical width. Vertex width 1.0–1.1× length. Discal micropunctures of tergum II averaging two to three diameters apart. Punctures of tergum V sparse mesally. Length 6.5–9.0 mm.

♂.—Clypeus (Fig. 93b): lip obtusely triangular; free margin not angulate between lobe and lateral section; distance between lip corners about equal to clypeal length and to distance between corner and orbit. Dorsal length of flagellomere I 1.2–1.4× apical width. Vertex width 1.1–1.4× length. Sterna minutely punctate, punctures less than one diameter apart except more than one diameter apart on apical depression. Length 5.2–6.2 mm.

Sternal pubescence velvety, concealing integument or nearly so.

GEOGRAPHIC DISTRIBUTION (Fig. 94).—Alberta, California, southern Utah, southern Arizona, Baja California, and Chihuahua State in Mexico, and also northwestern Nebraska. The species occurs in a variety of habitats, from sandy arroyos with cacti in central Baja California to grassy hills north of San Francisco, California.

COLLECTING PERIOD.—18 March to 6 May and 7 October (Baja California), 20 September (Chihuahua), 2 May to 28 September (United States and Canada).

MATERIAL EXAMINED.—Holotype: ♂, Mexico: Baja California Sur: Los Barriles, 3–4 May 1979, MSW (CAS, Type #14205)

Paratypes (62♀, 53♂): CANADA: **Alberta:** Drumheller, TLG (1♂, CAS).

UNITED STATES: ARIZONA: **Cochise:** 2 mi W Portal, WJP (1♀, CAS). **Pima:** Tucson, FDP and LAS (1♀, UCD). **Pinal:** Boyce Thompson Arboretum 3 mi W Superior, WJP (3♀, 3♂, CAS). CALIFORNIA: **Alameda:** Patterson Reserve, Del Valle Lake, JAP (1♀, CIS); no specific locality, J. C. Bridwell (1♂, USNM). **Contra Costa:** Canyon, W. R. Kellen (1♀, CIS), Danville, FXW (1♀, CAS); Mt. Diablo, FXW (3♂, CAS); San Pedro Reservoir, G. C. Eickwort (1♀, CU). **Inyo:** Surprise Canyon, PMM (1♂, UCD). **Marin:** 2 mi NE Bolinas, G. I. Stage (1♂, LACM); Mt. Tamalpais State Park, WJP (9♀, 10♂, CAS; 2♀, 2♂, MCZ; 1♀, 1♂, Zool. Mus. Copenhagen); San Rafael, collector unknown (3♀, 4♂, UCD; 1♀, 2♂, WJP); no specific locality, FXW (1♂, CAS). **Riverside:** Riverside, J. Hall (1♀, CAS; 2♀, UCR). **San Bernardino:** Providence Mts., TLG (1♂, TLG); Wildwood Canyon 3 mi E

Yucaipa (1♂, TLG). **San Diego:** Chihuahua Valley, EIS (1♂, UCD); Chula Vista, H. A. Dozier (1♂, UMMZ); La Mesa, FXW (2♀, CAS), Mission Gorge, R. B. Parks (1♀, SDNH). **San Mateo:** Redwood City, FXW (3♂, UCD). **Santa Clara:** Palo Alto, collector not indicated, gaster missing (1♂, LACM). **Sonoma:** Glen Ellen, RMB (1♂, UCD). **Stanislaus:** Del Puerto Canyon, PHA (1♂, CAS). NEBRASKA: **Dawes:** Chadron, R. W. Dawson (3♀, UCD; 1♀, WJP; 2♀, WSU). **Sheridan:** Rushville, R. W. Dawson (1♀, WSU). **Sioux:** Sawbelly Canyon, R. W. Dawson (1♂, UCD), same locality and collector, paratypes of *Tachysphex angularis* Mickel (2♂, CU, UNL). UTAH: **Garfield:** Capitol Reef National Park, Sulphur Creek, Lindahl (1♀, USU).

MEXICO: **Baja California Norte:** Arroyo del Rosario (3 mi above El Rosario), H. B. Leech and PHA (1♀, CAS); Cataviña, WJP (2♂, CAS); 4.6 mi SE Colonet, DKF (1♂, SDNH); El Portezuelo (39 road mi S Cataviña), WJP (2♀, CAS); 8 mi NE El Rosarito (28°44′N, 113°56′W), WJP (1♀, CAS); 1–3 mi SE Santa Rosalillita (28°44′N, 114°08′W), WJP (1♀, CAS). **Baja California Sur:** 30 mi ESE Bahía Tortugas, WJP (1♂, CAS); La Paz, FXW (1♂, CAS); Los Barriles, MSW (3♀, 1♂, CAS; 13♀, 2♂, CSDA); 7.7 mi NE San Isidro, N. Bloomfield and DKF (1♂, SDNH). **Chihuahua:** 5 mi N Escalón, RMB (1♀, 1♂, UCD). Also: "Harry A. Hill collector, 15 July 1942" (1♀, SDNH).

Tachysphex arizonac Pulawski

(Figures 95, 96)

Tachysphex arizonac Pulawski, 1982:30, ♀, ♂. ! Holotype: ♂, Arizona: Cochise Co.: 2 mi NE Portal (UCD)

DIAGNOSIS.—*Tachysphex arizonac* has well-defined mesopleural punctures, transversely oriented midscutal setae, and a horizontal depression at the apex of sternum I. The clypeal free margin of the female is either undulate, or with an obtuse, median projection (Fig. 95a). Females with an undulate clypeal margin are not easily separated from *lamellatus,* but a useful character is the hypostomal carina which is low in *arizonac,* but high in many *lamellatus.* The male of *arizonac* has a distinctive clypeus (Fig. 95b): the bevel is semilunate, the lobe forecorner is prominent (acutely in some specimens), and the lip of many specimens has an obtuse, median projection. The clypeus is somewhat similar in *texanus* and some *yolo,* but the vestiture is different. In *texanus,* mesopleural setae are appressed or nearly so beneath the scrobe (setae suberect in *arizonac*), and *yolo* has a nonvelvety sternal pubescence (sternal pubescence velvety in most *arizonac*).

DESCRIPTION (see also Table 2 under *texanus,* p. 123).—Punctures subcontiguous on scutum, but many discal punctures up to two to three diameters apart in females and many males; on vertex varying from about one to partly two to three diameters apart. Mesopleural punctures less than one diameter apart or (some specimens) about one diameter apart below scrobe. Propodeal dorsum irregularly rugose to evenly reticulate.

Vestiture obscuring integument between antennal socket and orbit. Setae about 1.3 MOD long on vertex; on scutum suberect, about 1.3 MOD long anterolaterally; suberect on hypoepimeral area.

Legs black, tarsal apex reddish; gaster all red (most specimens) to all black, in many specimens red with black, irregular spots. Terga I–IV (I–III in some females) silvery fasciate apically. Wings almost hyaline.

♀.—Clypeus (Fig. 95a): bevel as long as basomedian area or shorter; free margin of lip undulate, with obtuse, median projection, and also with obtuse, sublateral projection on each side (median projection in some specimens markedly larger than sublateral one). Dorsal length of flagellomere I 1.8–2.5× apical width. Vertex width scarcely more to scarcely less than length. Discal micropunctures of tergum II averaging two to three diameters apart. Tergum V densely punctate or punctures sparse mesally. Length 9.5–11.0 mm.

FIGURE 94. Geographic distribution of *Tachysphex huchiti* sp. n

♂.—Clypeus (Fig. 95b): bevel semilunate, shallowly concave in some specimens; lip usually with obtuse projection mesally, but simply arcuate in some specimens; lobe forecorner prominent, mostly acute. Dorsal length of flagellomere I 1.3–1.9× apical width. Vertex width 1.2–1.3× length. Sterna evenly, mi-

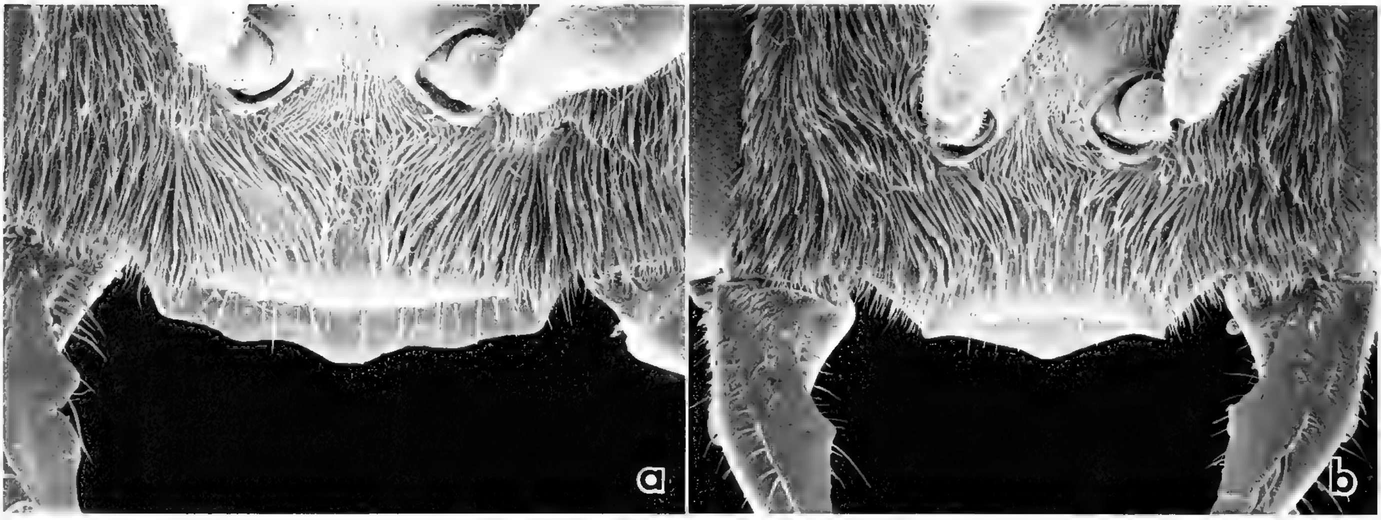

FIGURE 95. *Tachysphex arizonac* Pulawski: a—female clypeus; b—male clypeus.

nutely punctate (punctures less than one diameter apart), but sterna II–V apically impunctate, glabrous. Length 7–8 mm.

Sternal pubescence velvety but thin in many specimens in which the integument is easily visible.

GEOGRAPHIC DISTRIBUTION (Fig. 96).—Arizona, Utah, southern and central California, southern New Mexico, southwestern Texas, northern and central Mexico.

MATERIAL EXAMINED.—43♀, 33♂ (AMNH, ASU, CAS, CIS, CSDA, FSCA, LACM, NSDA, NYSU, SDNH, UAT, UCD, UCR, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** 6 mi NE Apache, Elfrida, Huachuca Mts., 2 mi NE Portal. **Graham:** Roper Lake State Park (6 mi S Safford). **Maricopa:** Phoenix, 3 mi SW Wickenburg. **Pima:** Brown Canyon (Baboquivari Mts.), Santa Catalina Mts. (Molino Basin, Sabino Canyon), Santa Rita Mts. (Sycamore Canyon), Sierritas (31°56′N, 111°16′W), Tucson. **Santa Cruz:** Madera Canyon, Sycamore Canyon (Atascosa Mts.), Tumacacori Mts. **Yuma:** Mohawk (3 mi W Wellton). CALIFORNIA: **Imperial:** Experimental Farm. **Inyo:** Big Pine, Deep Springs. **Merced:** 2 air mi SE Mariposa Peak. **Riverside:** Upper Deep Canyon at Horsethief Creek. **San Diego:** Anza-Borrego Desert State Park (Grapevine Canyon), Descanso. **Stanislaus:** Del Puerto Canyon. NEVADA: **Clark:** Juanita Springs (10 mi S Riverside). NEW MEXICO: **Dona Ana:** Leasburg Dam State Park. TEXAS: **Brewster:** Big Bend National Park (Trap Spring, Tornillo Creek). UTAH: **Uintah:** SW Bonanza. **Washington:** Leeds Canyon, Rockville, Santa Clara, Snow Canyon, Toquerville, Zion National Park.

MEXICO: **Baja California Norte:** Cataviña. **Baja California Sur:** 4 mi WSW Miraflores. **Sinaloa:** 8 mi SE Elota. **Sonora:** Cocorit, La Aduana.

Tachysphex lamellatus Pulawski

(Figures 97, 98)

Tachysphex lamellatus Pulawski, 1982:32, ♀, ♂. ! Holotype: ♂, Mexico: Sonora: Alamos (CAS, Type #13465).

DIAGNOSIS.—*Tachysphex lamellatus* has a punctate mesopleuron, the midscutal setae are transversely oriented, and sternum I has a horizontal depression apically. The male has a triangular or subtriangular clypeal lip (Fig. 97b) and a nondentate inner mandibular margin (Fig. 97b). All these characters are identical in males of *huchiti* and *sonorensis*. In *lamellatus*, however, scutal setae are nearly erect, 1.3 MOD long anterolaterally, and flagellomeres I–III are the usual length, whereas in *huchiti* scutal setae are subappressed, shorter than MOD, and in *sonorensis* flagellomeres I–III are shortened. The female of *lamellatus* has a distinctive, undulate clypeal lip (Fig. 97a), but many *arizonae* have the same clypeus, and such individuals cannot be separated with certainty from *lamellatus*. Two characters help in recognition of *lamellatus*: the hypostomal carina is unusually high in some females and most males (as it is in *paiute*), and the gena adjacent to the hypostoma is ridged in most males (Fig. 97c). Such ridges have not been found in any other *Tachysphex*.

DESCRIPTION (see also Table 2 under *texanus*, p. 123).—Scutal punctures less than one diameter apart on scutum, but many punctures of disk two to three diameters apart in some females. Mesopleural punctures varying from about one to two or three diameters apart below scrobe. Propodeal dorsum irregularly rugose to evenly reticulate, side punctate in some males.

Vestiture concealing sculpture between antennal socket and orbit.

Legs black, tarsal apex brown. Gaster red, but tergum I black in male from Atascosa Mountains, Arizona, and terga V–VII and all sterna largely black in male from Sabino Canyon, Arizona. Terga I–IV (I–III in some females) silvery fasciate apically. Wings almost hyaline.

♀.—Clypeus (Fig. 97a): bevel about as long as basomedian area; free margin of lip undulate, with obtuse, median projection, and one obtuse, sublateral projection on each side. Dorsal length of flagellomere I 2.0–2.4× apical width. Vertex width scarcely more to scarcely less than length. Vertex punctures varying from less than one to mainly two or three diameters apart. Discal micropunctures of tergum II varying from about one to two or three diameters apart. Tergum V densely punctate or punctures sparse mesally. Length 7.0–9.5 mm.

Setal length 1.0–1.3 MOD on vertex and anterolaterally on scutum; scutal setae subappressed or erect.

♂.—Clypeus (Fig. 97b): free margin not angulate or scarcely angulate between lip and lateral section; lip obtusely angulate, but rounded in some small individuals; distance between corners more than to less than distance between corner and corresponding orbit. Dorsal length of flagellomere I 1.0–1.3× apical width. Vertex width 1.3–1.6× length. Sterna evenly, minutely punctate (punctures less than one diameter apart) except impunctate, glabrous apically. Length 5–8 mm.

Setal length (in MOD): 1.0–1.3 on vertex; 1.3 on scutum anterolaterally (setae suberect); 1.5–2.0 on mesopleuron (setae suberect). Sternal setae velvety but thin, integument easily visible.

VARIATION.—The hypostomal carina is lamelliform in most specimens (Fig. 97c), two to several times higher than the occipital carina dorsally, forming an acute angle with the adjacent gena, but the carina is the usual form (as high as occipital carina dorsally) in many Arizona females, a single female from Cajon, California, a single female from Valle de Mazapa, Mexico, one of the males from Ramsey Canyon, Arizona, and two males found 3 mi SE Petlalcingo, Mexico.

In most males the gena is irregularly ridged adjacent to the hypostomal carina (Fig. 97c); the ridges are coarse in Mexican and some Arizona individuals, moderate or fine in most Arizona individuals, and absent in specimens from California, some from Arizona, and two males found 3 mi SE Petlalcingo, Mexico. All three conditions occur in males from Portal, Arizona.

GEOGRAPHIC DISTRIBUTION (Fig. 98).—New Mexico to southern California, north to southwestern Utah, Mexico.

MATERIAL EXAMINED.—150♀, 80♂ (CAS, CIS, CNC, FSCA, KU, NYSU, TLG, UAT, UCD, UCR, UIM, UMMZ, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** Paradise, Portal (also 5 mi S, 5 mi W, 5 mi SW), Ramsey Canyon (Huachuca Mts.). **Gila:** Gila River 3 mi SW Christmas. **Maricopa:** Gila River 7 mi S Buckeye. **Mohave:** Wikieup. **Pima:** Baboquivari Mts. (Brown Canyon, Elkhorn Ranch), Madrona Ranger Station (Rincon Mts.), Santa Catalina Mts. (Molino Camp, Sabino Canyon), Santa Rita Mts. (Madera Canyon, Sycamore Canyon), Tucson (also 5 mi N). **Pinal:** Superior (Boyce Thompson Arboretum). **Santa Cruz:** Atascosa Mts., Patagonia (also 12 mi SW), Santa Rita Mts. (Florida Canyon, Madera Canyon), Sycamore Canyon (Tumacacori Mts.). **Yavapai:** Irving Power Station (W Strawberry), Prescott. CALIFORNIA: **Inyo:** Darwin Falls. **Orange:** Laguna Canyon. **San Bernardino:** Cajon Pass, Mid Hills (9 mi SSE Cima). NEW MEXICO: **Catron:** Glenwood. **Luna:** 6 mi NW Florida. UTAH: **Washington:** Leeds Canyon, Zion National Park (Birch Canyon).

MEXICO: **Chiapas:** Valle de Mazapa. **Chihuahua:** 6 mi S Encinillas. **Hidalgo:** Jacala. **Puebla:** 3 mi NW Petlalcingo (also 3 mi SE). **Sinaloa:** 9 mi E Chupaderos, 54 mi S Culiacán. **Sonora:** Alamos, La Aduana. **Tres Marias Island:** Maria Magdalena Island

Tachysphex tsil sp. n.

(Figures 99, 100)

DERIVATION OF NAME.—Tsil is an Apache word for mountain; noun in apposition. An allusion to the Chiricahua Mountains where the holotype was collected (the name of this range is derived from the Apache words tsil, mountain, and kawa, great).

DIAGNOSIS.—*Tachysphex tsil* has well-defined mesopleural punctures, midscutal setae oriented laterad or posterolaterad, and an apical depression on sternum I. Several other species share these characters, but the male of *tsil* has a distinctive clypeus (Fig. 99): the lip is markedly sinuate, and the distance between its corners equals 0.7–0.8 of the clypeal length (greater than clypeal length in other species). In the female, mesopleural punctures average more than one diameter apart beneath the scrobe. This condition is also found in *sonorensis* and some *lamellatus*. The female of *lamellatus* can be recognized by its distinctive, undulate clypeal lip (Fig. 97a), and most specimens have an unusually high hypostomal carina (Fig. 97c). Females of *tsil* and *sonorensis* apparently are inseparable, differing only in size (8.0–8.5 mm in *tsil*, 9–11 mm in *sonorensis*). The geographic ranges help in their identification: both occur in Mexico, but *tsil* ranges north into Arizona and Oklahoma, while *sonorensis* ranges from Costa Rica to North Dakota and Oregon. Furthermore, *tsil* is an uncommonly collected species.

FIGURE 96 Geographic distribution of *Tachysphex arizonac* Pulawski

DESCRIPTION (see also Table 2 under *texanus*, p. 123).—Punctures almost contiguous on scutum in most specimens, but many

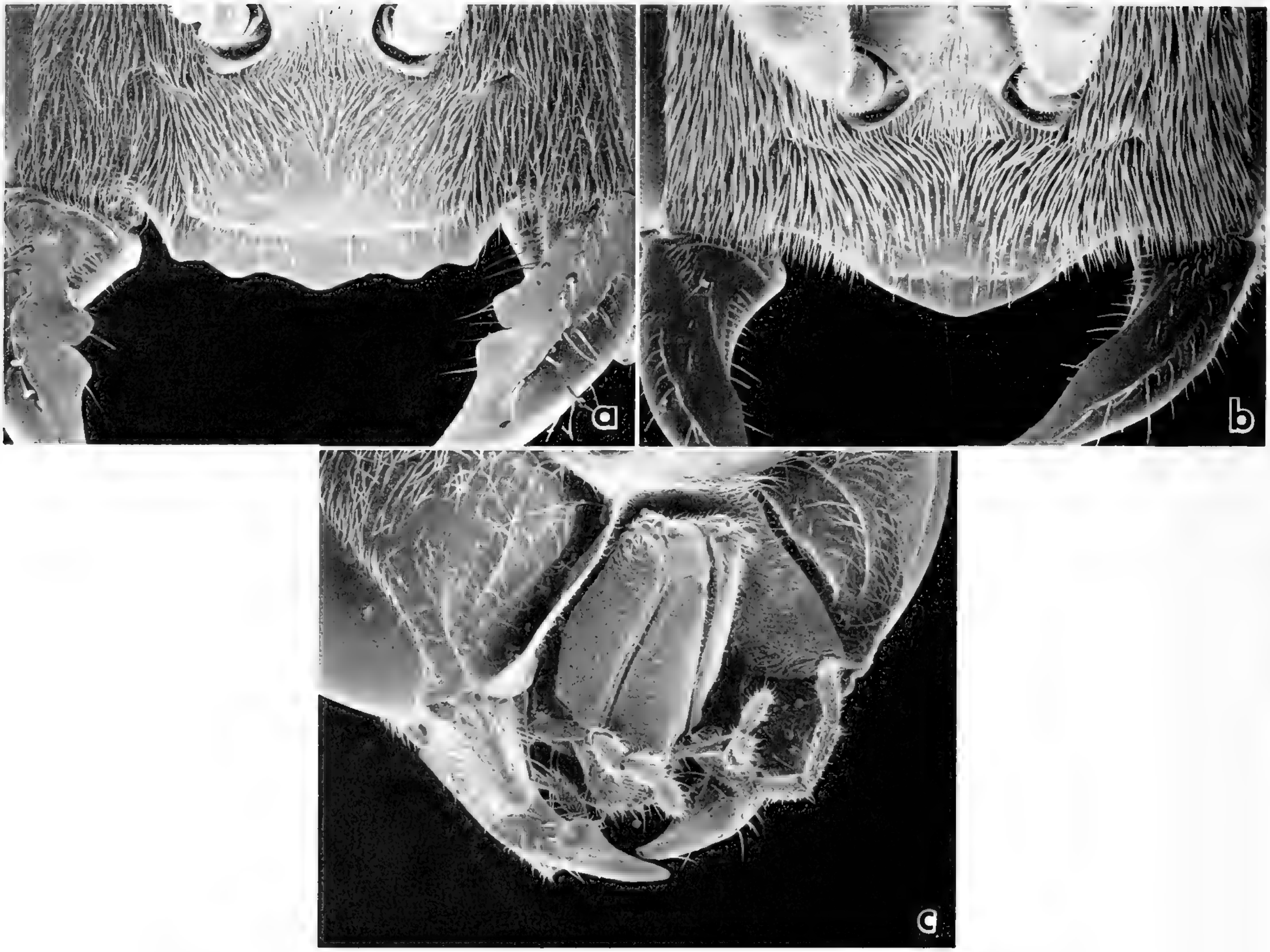

FIGURE 97 *Tachysphex lamellatus* Pulawski: a—female clypeus; b—male clypeus; c—male mouthparts and adjacent areas.

diameters apart on each side of median zone in the single female from Oklahoma; on vertex unevenly distributed, subcontiguous to two or three diameters apart, on mesopleuron averaging more than one diameter apart below scrobe in females and most males (one diameter in the single male from Kingman area, Arizona) and most males. Propodeal dorsum rugose.

Vestiture not totally obscuring integument between antennal socket and orbit. Setae 1.0–1.4 MOD long on vertex; on scutum erect (1.3 MOD long) to nearly appressed (1.0 MOD long) anterolaterally, erect on hypoepimeral area.

Legs black, tarsal apex reddish; gaster red. Terga I–III or I–IV silvery fasciate apically. Wings almost hyaline.

♀.—Clypeus: bevel about as long as basomedian area; lip varying: evenly arcuate, obtusely pointed, or obtusely prominent mesally and sublaterally (free margin undulate). Dorsal length of flagellomere I 2.0–2.2 × apical width. Vertex width 1.0–1.25 × length. Discal micropunctures of tergum II averaging one to three diameters apart. Tergum V sparsely punctate. Length 8.0–8.5 mm.

♂.—Clypeus (Fig. 99): distance between lip corners 0.7–08 of clypeal length and about 0.6 of distance between corner and orbit; lip with obtuse median prominence, its forecorner prominent, acute (free margin markedly sinuate). Dorsal length of flagellomere I 1.3–1.5 × apical width. Vertex width 1.15–1.4 × length. Sterna evenly, minutely punctate (punctures less than one diameter apart), but sterna II–VI apically impunctate, glabrous. Length 6.0–7.0 mm.

Sternal pubescence velvety.

DISCUSSION.—Females of *tsil* and *sonorensis* are indistinguishable, and my association of sexes in *tsil* is based on the following: (1) males and females have identical basic structures such as mesothoracic sculpture and vestiture and the shape of sternum I, and (2) both females and males were collected together in certain localities where *sonorensis* has not been found (e.g., in Portal area, Arizona, Black Mesa State Park, Oklahoma, or near Perote, Mexico).

GEOGRAPHIC DISTRIBUTION (Fig. 100).—Known from Arizona, Oklahoma panhandle, as well as Jalisco, Morelos, and Veracruz states in Mexico.

COLLECTING PERIOD.—24–29 February, 6 and 14 March

FIGURE 98. Geographic distribution of *Tachysphex lamellatus* Pulawski.

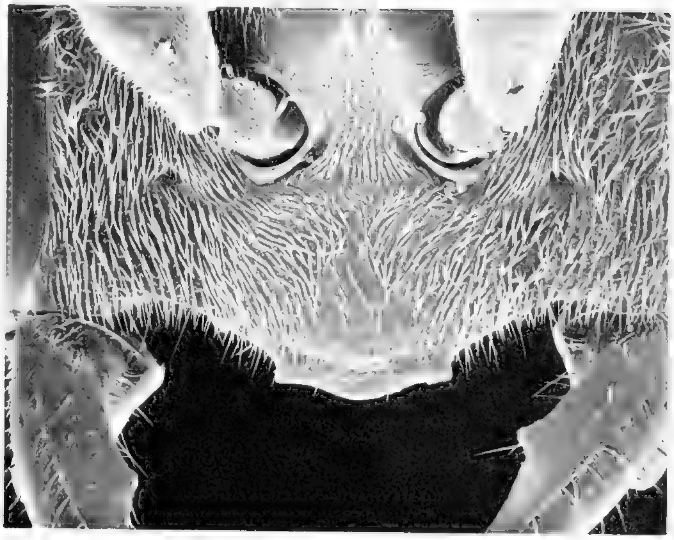

FIGURE 99. *Tachysphex tsil* sp. n.: male clypeus.

(Mexico); 12 March (Kingman area, Arizona); 5–20 May, 29 June, 7 September to 28 October (remaining Arizona localities and Oklahoma).

MATERIAL EXAMINED.—Holotype: ♂, Arizona: Cochise Co.: 5 mi W Portal, Southwestern Research Station, 6 October 1966, PHA (CAS, Type #14161).

Paratypes (7♀, 14♂): UNITED STATES: ARIZONA: **Cochise:** Hidden Terrace in Chiricahua Mts., 4.5 mi W Portal, M. Cazier (1♀, AMNH); 5 mi W Portal, Southwest Research Station, J. G. Rozen (2♀, AMNH, CAS), V. Roth (1♀, AMNH), M. Statham (1♂, UCD); 6 mi W Portal, A. L. Steiner (1♀, 1♂, UAE; 1♂, CAS). **Maricopa:** 3 mi SW Wickenburg, P. Torchio and GEB (2♂, UCD, USU). **Mohave:** 8 mi N Kingman, P. Torchio and B. Appleton (1♂, USU). **Pima:** Sabino Canyon, JWMS (1♂, CIS). OKLAHOMA: **Cimarron:** Black Mesa State Park, WJP (1♀, 1♂, CAS).

MEXICO: **Jalisco:** Laguna de Moreno, RCB and EIS (2♂, CAS, UCD). **Morelos:** 3 and 4 mi N Cuernavaca, HEE (2♂, CU). **Veracruz:** 5 mi SW Perote, FDP and D. Miller (1♂ CAS; 1♀, 1♂, USU).

Tachysphex sonorensis (Cameron)

(Figures 101, 102)

Larra sonorensis Cameron, 1889:50, ♀. ! Holotype: ♀, Mexico: northern Sonora: no specific locality (BMNH).—In *Tachysphex:* Bohart and Menke 1976:276; Krombein 1979:1629; Rust et al. 1985:46, 53; Parks 1986:34.

Tachysphex dakotensis Rohwer, 1923:98, ♀. ! Holotype: ♀, North Dakota: Bowman Co.: Gascoyne (USNM). Synonymized by Pulawski *in* Krombein 1979:1629.—G. Bohart 1951:951; Bohart and Menke 1976:273.

Tachysphex schlingeri R. Bohart, 1962:36, ♂, ♀. ! Holotype: ♂, California: Sierra Co.: Sierraville (CAS). Synonymized by Pulawski *in* Krombein 1979:1629.—Krombein 1967:393; Bohart and Menke 1976:276

DIAGNOSIS.—*Tachysphex sonorensis* has well-defined mesopleural punctures, the midscutal setae oriented transversely or posterolaterad, and sternum I has a well-defined, horizontal depression apically. *Tachysphex texanus, huchiti, yolo,* and *yuma* are similar, but in *sonorensis* the mesopleural punctures average more than one diameter apart below the scrobe (Fig. 101a, b), and the setae are almost erect on the scutum and hypoepimeral area. The females of *sonorensis* and *tsil* are identical morphologically, but they differ in size and their geographic ranges help in identification (see *tsil* for details). *Tachysphex amplus, arizonac,* and *lamellatus* are also similar, but their clypeus is distinctive (see these species for other differences). The male of

FIGURE 100. Geographic distribution of *Tachysphex tsil* sp. n.

sonorensis has a distinctive flagellum (Fig. 101e): flagellomeres I–III shortened, I about as long ventrally as pedicel, III about 0.75 length of IV. Additional recognition features in the male are: clypeal lip triangular (Fig. 101c), inner mandibular margin not dentate (Fig. 101d), forebasitarsus with preapical rake spines (rudimentary in some individuals), and sternal pubescence not velvety.

DESCRIPTION (see also Table 2 under *texanus*, p. 123).—Vertex and mesothorax punctate. Mesopleural punctures averaging more than one diameter apart below scrobe (Fig. 101a, b). Propodeal dorsum areolate or rugose.

Setae 1.0–1.1 MOD long on vertex; erect on hypoepimeral area, suberect to subappressed below mesopleural scrobe.

Legs black, tarsal apex brown or reddish. Gaster red (most specimens) to black. Terga I–III or I–IV silvery fasciate apically. Wings weakly infumate to almost hyaline.

♀.—Clypeus: bevel triangular, as long mesally as basomedian area or longer; lip arcuate or weakly undulate. Dorsal length of flagellomere I 1.8–2.2× apical width. Vertex width equal to length or slightly more; punctures one to two diameters apart. Most scutal punctures usually several diameters apart on each side of mesal zone, but one to two diameters apart in some specimens. Discal micropunctures of tergum II at least two diameters apart. Punctures of tergum V two to four diameters apart mesally. Length 9–11 mm.

Scutal setae suberect, 0.8–0.9 MOD long anterolaterally.

♂.—Clypeus (Fig. 101c): bevel delimited laterally by short, longitudinal carina that extends from lip corner; lip triangular, its corners rounded, closer to each other than to orbit or equidistant. Dorsal length of flagellomere I 0.9–1.1× apical width, ventral length equal to pedicellar venter or slightly less (Fig. 101e); length of flagellomere III about 0.75 of IV. Vertex width 1.4–1.7× length. Vertex punctures one to three diameters apart. Scutal punctures (some specimens) less than one diameter apart or (most specimens) many discal punctures one to three diameters apart. Sterna evenly, minutely punctate (punctures less than one diameter apart) except sterna II–V apically impunctate, glabrous. Outer margin of foretarsomere I with two to five preapical spines whose length may exceed tarsomere width. Length 6–10 mm.

Scutal setae erect, 0.9–1.0 MOD long. Sternal pubescence not velvety, integument easily visible.

VARIATION.—The gaster varies from all red to all black. The black form occurs mainly in mountains; it was described as *dakotensis* by Rohwer (1923) and as *schlingeri* by R. Bohart (1962). On Santa Rosa Island, California, the gaster is all red in females and all black in males. The gaster is red in both sexes on Santa Cruz Island.

GEOGRAPHIC DISTRIBUTION (Fig. 102).—Alberta, North Dakota and Oregon to Panama.

MATERIAL EXAMINED.—235♀, 289♂.

RECORDS (b: gaster all black).—CANADA: **Alberta:** Drumheller (b).

UNITED STATES: ARIZONA: **Cochise:** 15 mi SW Apache, 17 mi E Douglas (also 20 mi N), Hereford. **Maricopa:** Phoenix, Tempe. **Mohave:** Kingman. **Pima:** Organ Pipe Cactus National Monument. **Santa Cruz:** Nogales. **Yavapai:** 8 mi NE Yarnell. CALIFORNIA: **Alpine:** Hope Valley (b), Winnemucca Lake. **Contra Costa:** Danville, Moraga. **El Dorado:** 5–6 mi NE on Icehouse road (24 air mi ENE Placerville—b), Lake Fontanillis, 8,500 ft (b), South Lake Tahoe (b). **Fresno:** Firebaugh, Fresno. **Humboldt. Imperial:** —. **Inyo:** Bishop (also 15 mi N), Deep Springs, 2 mi S Lone Pine. **Kern:** Mill Potrero, 13 mi S Shafter. **Lassen:** Bridge Creek Camp, Hallelujah Junction (b). **Los Angeles. Marin. Mendocino. Merced:** Dos Palos, George J. Hatfield State Park. **Modoc:** Lake City. **Mono. Monterey:** Asilomar, Pacific Grove. **Nevada:** Boca (partly b), Sagehen Creek near Hobart Mills (partly b). **Orange. Placer:** 4 mi S Rocklin. **Riverside:** Anza, Calimesa, Temecula. **San Bernardino:** Hole-in-the-Wall (Providence Mts.), Saratoga Springs, 3 mi SE Yucaipa. **San Diego. San Francisco:** San Francisco (Lone Mountain). **San**

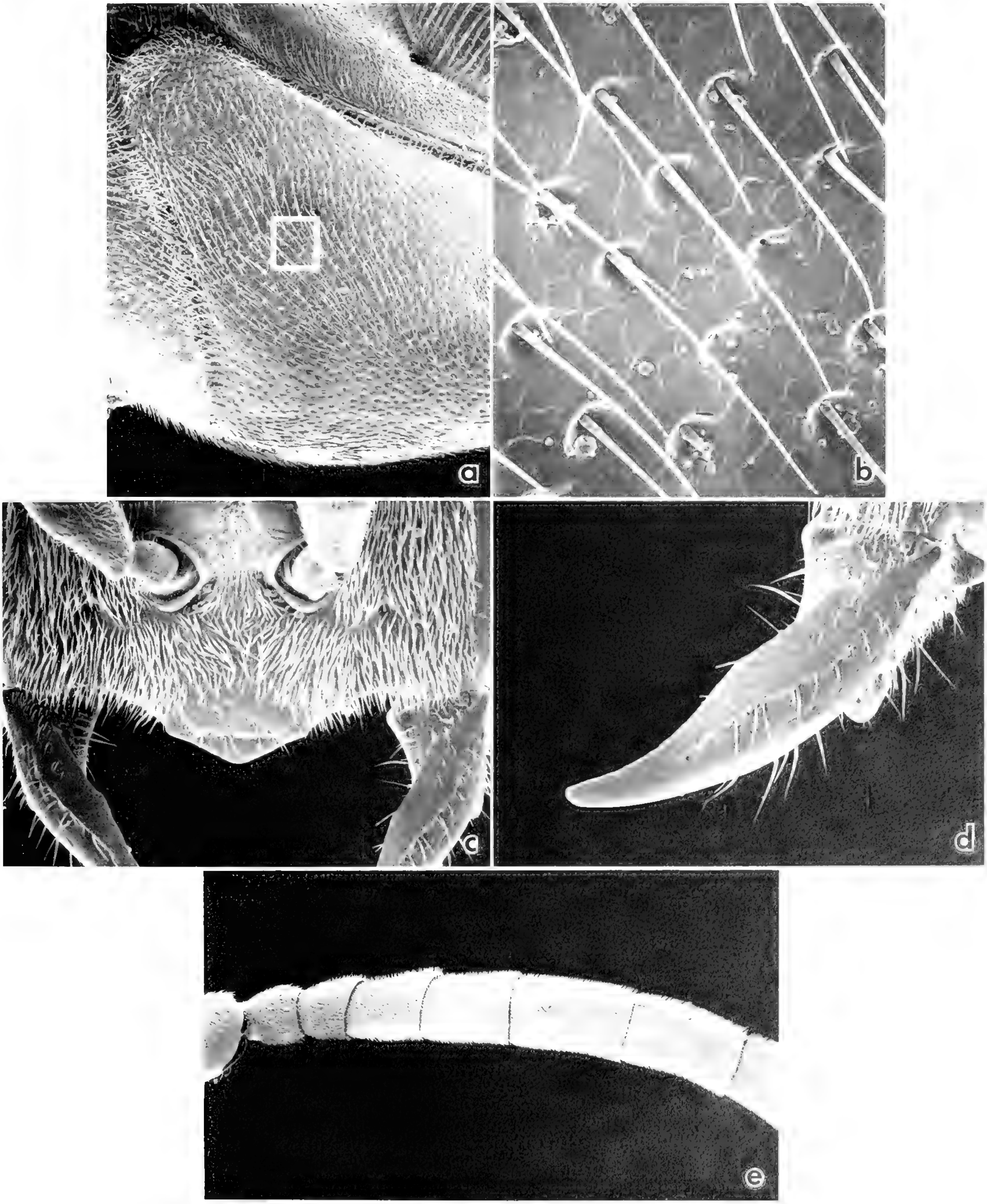

FIGURE 101. *Tachysphex sonorensis* (Cresson). a—female mesopleuron (box: area shown in b), b—mesopleural punctures shown in box of a, c—male clypeus, d—male mandible, e—male antenna.

FIGURE 102. Geographic distribution of *Tachysphex sonorensis* (Cresson).

Joaquin: Corral Hollow (8 mi SW Tracy), Hospital Canyon, Weston. **San Luis Obispo. San Mateo:** Half Moon Bay (also 12 mi N), Redwood Canyon, Redwood City. **Santa Barbara:** including Santa Cruz Island and Santa Rosa Island. **Santa Clara:** Croy road, San Jose, Stanford University. **Shasta:** Redding. **Sierra:** Independence Lake (partly b), Sardine Creek ca. 1 mi NW Bassets (partly b), Sattley, Sierraville (partly b). **Siskiyou:** Bull Meadow, Etna, Klamath River 8 mi N Yreka. **Solano:** Putah Creek. **Sonoma. Stanislaus:** Modesto, Newman. **Tehama:** Colyear Springs Road. **Trinity:** Cedar Creek. **Tulare:** Woodlake. **Tuolumne:** Dodge Ridge near Strawberry (R. Bohart 1962—b), Don Pedro Reservoir (9 air mi W Coulterville), Leland Meadow. **Ventura. Yolo:** Davis. COLORADO: **Larimer:** Masonville. IDAHO: **Bear Lake:** Montpelier (b). **Butte:** Craters of the Moon National Monument. **Canyon:** 2 mi N Melba, Parma. **Elmore:** 3 mi SE Mt. Home. **Gooding:** 1 mi NE Gooding. **Lincoln:** Owinza Hot Springs. **Twin Falls:** Rogerson. KANSAS: **Barber:** 2.5 mi S Aetna, 16 mi W Hardtner. NEVADA: **Churchill:** Fallon. **Clark:** Overton. **Elko:** Wild Horse. **Humboldt:** Orovada. **Lyon:** Fernley. **Washoe.** NEW MEXICO: **Dona Ana:** Leasburg Dam State Park. **Luna:** 17 mi E Deming. **Otero:** Alamogordo. **Torrance:** Moriarty. NORTH DAKOTA: **Bowman:** Bowman, Gascoyne (b). OREGON: **Curry:** Brookings, 6–10 mi E along Winchuck River. **Klamath:** Lower Klamath Lake (partly b). **Sherman:** Rufus. TEXAS: **Bexar, Bosque:** —. **Hidalgo:** McAllen Botanical Garden. UTAH: **Cache:** Cornish, Green Canyon, Smithfield. **Millard:** Delta. **Uintah:** SW Bonanza (partly b). **Washington:** 1 mi W Leeds, Leeds Canyon. WYOMING: **Sweetwater:** Green River (R. Bohart 1962—b). **Teton:** Moran (b).

MEXICO: **Baja California Norte:** Arroyo Grande (39 mi SW La Ventana—b), Ensenada, Rio San Miguel (La Misión), Salsipuedes, 10 and 40 mi S San Quintin, 5mi S Santa Maria. **Baja California Sur:** La Paz, 6 mi S San Juanico, San Pedro. **Chihuahua:** 10 mi S Jiménez, Matachic. **Jalisco:** Estanzuela (40 km W Ameca), 25 mi N Guadalajara. **Puebla:** 7 mi NE Atlixco, 25 mi SE Puebla. **Sinaloa:** 19 mi S Villa Unión. **Sonora:** Alamos, Guaymas, Navajoa, 8 mi S Santa Rita.

CENTRAL AMERICA: COSTA RICA: **Guanacaste:** Rio Corbici near Cañas. PANAMA: El Volcan Chiriqui.

Tachysphex papago Pulawski

(Figure 104)

Tachysphex papago Pulawski, 1982:35, ♀, ♂. ! Holotype: ♀, Arizona: Santa Cruz Co.: Nogales (BMNH).

Diagnosis.—*Tachysphex papago* has a short malar space (rudimentary in some specimens), a punctate mesopleuron, and terga I and II are microsculptured and ciliate but contrastingly unsculptured and glabrous apicomesally. These characters are shared with *psilocerus* and *scopaeus,* but the upper metapleuron is simple in *papago,* and the metapleural flange is narrow (in the other two, the upper metapleuron is variously modified, and the flange is broad). In addition, the propodeal dorsum and side are punctate in *papago,* the basal (oriented posterad) setae of the propodeal dorsum extend almost from spiracle to spiracle, and the female flagellum is largely brown or red (these characters also occur in *psilocerus*). A subsidiary diagnostic feature is the presence of erect setae on the midfemoral venter (setae about 1.0 MOD long).

Description.—Malar space about 0.4 MOD long. Frons opaque, punctate, or punctatorugose. Punctures: averaging less than one diameter apart on frons, several diameters apart on vertex and mesothoracic venter; about one to several diameters apart on scutal disk; about one diameter apart or more on mesopleuron. Metapleuron punctate, upper metapleuron simple. Propodeum opaque, dorsum and side punctate (except side impunctate basally); dorsal punctures subcontiguous, interspaces in the form of minute, irregular, longitudinal ridges; side punctures averaging about one diameter apart, interspaces finely, longitudinally ridged; hindface punctate and irregularly, transversely ridged. Tergal micropunctures dense, but more than one diameter apart on disk of tergum II; terga I and II unsculptured apicomesally. Hindcoxa not carinate.

Setae erect on vertex and midfemoral venter, about 1.0 MOD long; scutal setae suberect, about 1.0 MOD long anterolaterally. Vestiture not concealing sculpture, except (when viewed from certain angles) between antennal socket and orbit and on basal half of propodeal dorsum. Setae of propodeal dorsum oriented anterad except oriented posterad on broad, basal zone that extends nearly from spiracle to spiracle.

Wings uniformly, moderately infumate to almost hyaline.

♀.—Clypeus: bevel longer than basomedian area; lip straight, obtusely produced mesally, but incised laterally. Dorsal length of flagellomere I 2.6–2.7× apical width. Vertex width about 1.4× length. Sternum I without apical depression or concavity. Apical depression of tergum V alutaceous, impunctate. Pygidial plate minutely punctate, interspaces smooth. Length 7 mm.

Body black, but the following red brown: mandible, clypeal lobe, antenna (except pedicel, flagellomere I basally, in some specimens also apical three flagellomeres), foretibia largely, midtibia, and all tarsi partly. Tergum I not fasciate, terga II and III fasciate apically (fasciae interrupted mesally).

♂.—Clypeus: lobe obtusely pointed, lip corners indistinct but slightly closer to each other than to orbits. Dorsal length of flagellomere I 1.4–1.5× apical width. Vertex width 1.6–1.8× length. Forebasitarsus without rake; outer apical spine of foretarsomere II about as long as tarsomere width. Forefemoral notch glabrous. Length 5.3–6.3 mm.

Body black except mandible reddish mesally. Terga I–IV fasciate apically (fasciae interrupted).

Geographic Distribution (Fig. 104).—Southern Arizona.

Material Examined.—3♀, 2♂ (BMNH, NYSU, UAE, WJP).

Records.—ARIZONA: **Cochise:** 5 mi W Portal (also 6 mi W). **Santa Cruz:** Nogales.

Tachysphex scopaeus sp. n.

(Figures 103, 104)

Derivation of Name.—Scopaeus is derived from the Greek word skopaios, a dwarf; noun in apposition.

Diagnosis.—*Tachysphex scopaeus* shares with *papago* and *psilocerus* a short malar space (rudimentary in some specimens), punctate mesopleuron, and a characteristic sculpture of terga I and II (microsculptured and ciliate but contrastingly unsculptured and glabrous apicomesally; Fig. 103e). However, *scopaeus* has a rugose propodeal dorsum and a ridged propodeal side (propodeal dorsum and side punctate in the other two); the posterad oriented setae on the propodeal dorsum are inconspicuous and present only basomedially (rather than extending almost from spiracle to spiracle); the hindcoxa has an expanded, toothlike carina dorsally (hindcoxa not carinate); and the male flagellomere III is about as long as 0.75 of flagellomere IV (0.9 of IV in the other two). In *scopaeus,* but also in *psilocerus,* the metapleural flange is broad (Fig. 103c, d), and the upper metapleuron is modified (the only two such cases in the *pompiliformis* group). The modifications are not identical: in *scopaeus,* there is an oblique lamella beneath the anterior end of the flange (Fig. 103c, d), and one or two longitudinal ridges behind the lamella (the ridges end before the propodeal spiracle). See *papago* and *psilocerus* for additional differences.

Description.—Malar space (Fig. 103b) about 0.5–0.8 MOD long. Frons with conspicuous microsculpture and shallow punc-

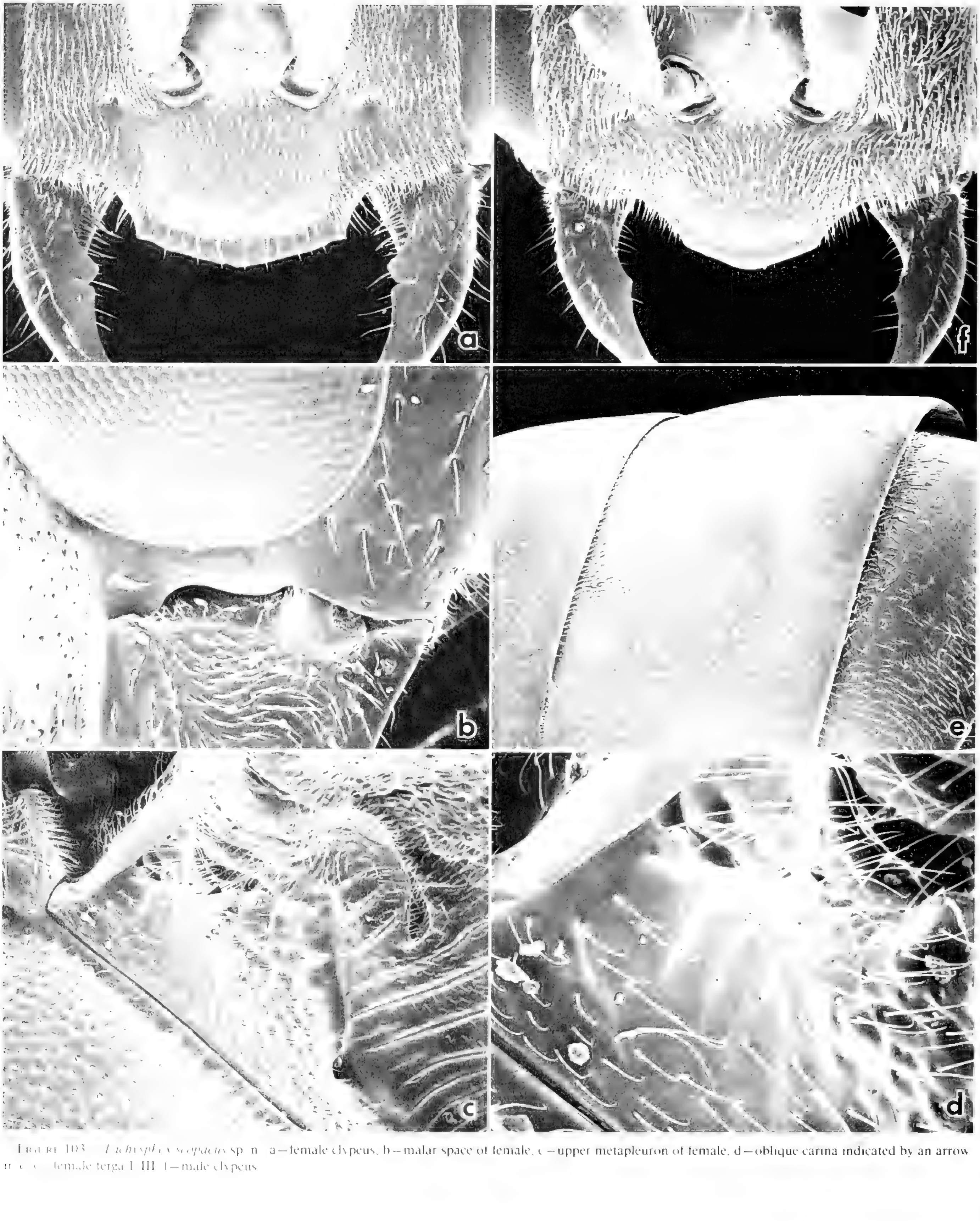

FIGURE 103. *Tachysphex scopaeus* sp. n.: a—female clypeus, b—malar space of female, c—upper metapleuron of female, d—oblique carina indicated by an arrow in c, e—female terga I–III, f—male clypeus.

tures that average up to one or two diameters apart. Vertex punctures one to many (female) or one to two (male) diameters apart. Scutal punctures varying from about one (males, some females) to many diameters apart (females from Junction, Dinosaur Valley, and Mason area). Mesopleuron opaque, its punctures well defined, up to two diameters apart posteriorly. Upper metapleuron (Fig. 103c, d) with short, oblique lamella that starts beneath anterior end of flange, and one or two horizontal carinae that start behind the lamella and end before propodeal spiracle; flange broad, almost as in *psilocerus,* overhanging metapleural surface posteriorly. Propodeal dorsum rugose, side and hindface ridged. Sternum I without apical depression. Discal micropunctures of tergum II several to many diameters apart. Terga I and II without any sculpture apicomesally (Fig. 103e). Hindcoxa carinate, carina expanded basally.

Setae erect, 1.0 MOD long on vertex; suberect, 1.0 MOD long on scutum (oriented evenly posterad mesally); appressed on midfemoral venter; not obscuring integument between antennal socket and orbit. Setae of propodeal dorsum oriented anterad, except a few inconspicuous basomedian setae that are oriented posterad.

Body black. Wings almost hyaline. Terga I–III or I–IV silvery fasciate apicolaterally.

♀.—Clypeus (Fig. 103a): bevel about as long as basomedian area, but large punctures extending over whole clypeal middle section in a female from Dinosaur Valley (fine, dense punctures absent); lip arcuate or sinuate, not emarginate mesally or incised laterally. Dorsal length of flagellomere I 2.0–2.2× apical width. Vertex width about 1.8× length. Tergum V with ill-defined micropunctures, its apical depression impunctate. Pygidial plate alutaceous, with a few sparse punctures. Length 6.5–7.0 mm.

Frontal vestiture golden.

♂.—Inner mandibular margin with tooth (Fig. 103f). Clypeus (Fig. 103f): lobe arcuate or obtusely triangular, its corners rectangular to widely obtuse, separated by a distance that equals 0.9 of clypeal length and 0.9 of distance from corner to orbit. Dorsal length of flagellomere I 0.9–1.0× apical width. Length of flagellomere III about 0.75 of IV. Vertex width 2.0–2.4× length. Forefemoral notch shiny, glabrous. Forebasitarsus with none to three preapical spines whose length does not exceed basitarsal width (the number of spines may be different on the right and the left tarsus). Length 5.0–5.5 mm.

Frontal vestiture silvery.

Discussion.—The presence of the malar space and the peculiar metapleural structure suggest that *psilocerus* and *scopaeus* do not belong to the *pompiliformis* group and that they ought to be placed in a group of their own. Actually *psilocerus* is related to *papago,* as evidenced by the overall body sculpture (especially of terga I and II) and the color of the female antennae. *Tachysphex papago,* with its unspecialized metapleuron and vestigial malar space, is thus a link between *psilocerus* and other members of the *pompiliformis* group.

Tachysphex papago, psilocerus, and *scopaeus* share the presence of a short malar space with the Old World *brevipennis* group. However, the absence of an episternal sulcus in that group, and its presence in *psilocerus, papago,* and *scopaeus* indicate that they are not related and that the malar space has been acquired independently.

Geographic Distribution (Fig. 104).—Southeastern Texas.

Collecting Period.—7–28 April, 2–17 May, 8–21 October, 4–11 November.

Material Examined.—Holotype ♀, Texas: Kleberg Co.: Kingsville, 1 April 1973, P. W. Treptow (UCD).

Paratypes (15♀, 22♂): TEXAS: **Brazos:** —, JEG (1♀, UCD). **Burleson:** Sommerville, Sal Nolfo (1♀, UMMZ). **Duval:** 8 mi W Premont, Gery Valle (1♀, TAI). **Hidalgo:** Bentsen Rio Grande Valley State Park, WJP (1♀, CAS). **Kenedy:** 27°09′N, 97°41′W, JEG (1♂, UCD; 1♀, 1♂, WJP). **Kimble:** Junction, WJP (1♀, CAS). **Kleberg:** Baffin Bay 6 mi E Riviera, JEG (1♂, UCD), 20 mi SE Kingsville, WJP (4♀, 1♂, CAS). **Mason:** 10 mi N Mason, Michener, Besmere, Wille, and LaBerge (1♀, UCD). **San Patricio:** 5 mi N Sinton, HEE and O. Flint (2♀, 1♂, MCZ), 10 mi NE Sinton on Aransas River, WJP (1♀, 5♂, CAS). **Somervell:** Dinosaur Valley State Park, WJP (1♀, 11♂, CAS). **Williamson:** Shiloh, JEG (1♂, UCD).

Tachysphex psilocerus Kohl

(Figure 104)

Tachysphex psilocerus Kohl, 1884:374, ♀. Holotype: ♀, Mexico: Chapultepec (Naturhist. Mus. Vienna, Austria, ?lost).—Cameron 1888–1900:64; Ashmead 1899: 250; Bohart and Menke 1976:276; Krombein 1979:1629.

Tachysphex helianthi Rohwer, 1911:570, ♀, ! Holotype: ♀, Colorado: Boulder (USNM). Synonymized by Pulawski *in* Krombein 1979:1629.—G. Bohart 1951 951; Bohart and Menke 1976:274.

Tachysphex nitelopteroides Williams, 1958:207, ♀, ♂, ! Holotype: ♀, Mexico: Baja California (Sur): La Paz (CAS). Synonymized by Pulawski *in* Krombein 1979 1629.—Arnaud 1970:32; Bohart and Menke 1976:275.

Diagnosis.—The following characters separate *psilocerus* and *papago* from other members of the *pompiliformis* group: the propodeal dorsum and side are punctate (dorsum laterally and side impunctate in some specimens); the posterad oriented basal setae of propodeal dorsum are conspicuous, extending almost from spiracle to spiracle; and the female flagellum is largely brown or red (also red in *pechumani*). The specialized metapleuron of *psilocerus* is distinctive: the flange is broad, and a longitudinal carina, about as long as the flange, is present just beneath it (metapleuron simple in *papago*). The only other species in the *pompiliformis* group with a specialized although not identical metapleuron is *scopaeus* (see that species for details). Other important characters of *psilocerus* (shared with *papago* and *scopaeus*) are the following: short malar space present (rudimentary in some specimens), mesopleural punctures well defined (minute in some specimens), and terga I and II are microsculptured and ciliate except contrastingly unsculptured and glabrous apicomesally. Unlike these two species, the forewing of *psilocerus* has a weak, transverse fascia.

Description.—Malar space present. Frons opaque, punctate, or punctatorugose. Punctures averaging less than one diameter apart on frons, about one diameter apart (or slightly less) on vertex and mesothorax, but varying on scutum. Upper metapleuron with oblique carina that starts at anterior end of flange and ends before propodeal spiracle. Metapleural flange broad, overhanging metapleural integument posteriorly. Propodeal dorsum opaque, with subcontiguous punctures (impunctate laterally in some females); side punctate (impunctate anteriorly in female, ridged basally in some males) or largely impunctate; hindface punctate (punctatorugose in some males). Tergal micropunctures dense, but more than one diameter apart on disk of tergum II; terga I and II without any sculpture apicomesally. Basal tooth of hindcoxa small or medium size. Hindcoxa not carinate.

Setae appressed on vertex and mesothorax. Vestiture not obscuring sculpture, except partly obscuring from certain angles

FIGURE 104. Geographic distribution of *Tachysphex papago* Pulawski, *psilocerus* Kohl, and *scopaeus* sp. n.

between antennal socket and orbit. Setae of propodeal dorsum oriented anterad except oriented posterad on broad, basal zone that extends almost from spiracle to spiracle.

♀.—Clypeus: bevel longer to shorter than basomedian area; lip not emarginate mesally nor incised laterally, evenly arcuate or (Portal female) obtusely projected mesally. Dorsal length of flagellomere I 2.7–3.2× apical width. Vertex width 1.6–1.8× length. Sternum I shallowly concave apicomesally. Apical depression of tergum V alutaceous, impunctate. Pygidial plate minutely punctate, interspaces alutaceous. Length 5.0–6.5 mm.

Color various (see Variation below). Tergum I not fasciate, terga II and III fasciate apicolaterally. Wings hyaline or nearly so, but forewing with slightly infumate, transverse band mesally. Frontal vestiture golden.

♂.—Mandibular inner margin not dentate. Clypeus: lobe arcuate; lip corners indistinct, as far from eyes as from each other. Dorsal length of flagellomere I 1.4–1.8× apical width. Vertex width about 1.9× length. Propodeal side punctate (interspaces microridged, about as broad as punctures) and finely, densely ridged basally, or largely impunctate. Foretarsus without rake; outer apical spine of foretarsomere II about as long as tarsomere width. Forefemoral notch shallow to evanescent (see Variation below). Length 5 mm.

Body black (most specimens) or partly red (Mexico, Wyoming); in the Sonora specimen the following are red: mandible (except apically), clypeus partly, scape, pedicel, flagellomeres I–III, pronotum, scutum partly, scutellum, mesopleuron partly, metapleuron, forecoxa, forefemur partly; tibiae yellowish-red. Wings hyaline.

VARIATION.—*Tachysphex psilocerus* varies considerably in the length of the malar space, sculpture, femoral setae, color, and shape of the male forefemur. Details are given below.

The malar space, at middle, is about 0.7 MOD long in most specimens, but about 0.3 MOD long in the females from Marfa, Texas; Huachuca Mountains, Arizona; and Nombre de Díos, Mexico.

Mesothoracic punctures are usually conspicuous (about as large as in most *psammobius*), but they are minute in Arizona females and a Sonora male.

Scutal punctures are one to two diameters apart in most specimens, but many diameters apart posteriorly in the single female from Arkansas. Most punctures are subcontiguous in Teotihuacán specimens, Huachuca and Portal females, and a Colorado male.

The metapleuron is punctate in most specimens, but is irregularly microrugose in an Apache female.

The metapleural flange is rounded apically or acutely expanded posterad (Arkansas, Colorado, and Durango).

The propodeal side is punctate (alutaceous anteriorly); partly unsculptured in Baja California specimens and an Apache female; or unsculptured (except partly alutaceous) in Texas, Huachuca, and Portal females, and in a Wyoming male.

The propodeal dorsum is impunctate laterally in females from Texas and Huachuca Mts. and Portal in Arizona.

The propodeal hindface is mostly punctate, but punctatorugose in a male from Park Creek, Colorado.

Setae of the midfemoral venter sparse and about 0.5–0.7 MOD long in most individuals but extremely short, dense, appressed in Baja California specimens, Apache and Huachuca females, and a Wyoming male.

The female head is all black (Colorado) or the clypeus and mandible (except apex) are red (Texas, Arizona, Mexico).

The female flagellum is red basally (apex of flagellomere I to base of flagellomere IV: Apache, Arizona, and Arkansas) or more extensively (flagellomeres I–VI: Portal, Arizona, and Texas).

The forefemoral notch is shallow in males from Poudre Canyon, Colorado; Wyoming; and Baja California, but evanescent in males from Teotihuacán and Park Creek, Colorado.

DISCUSSION.—Dr. M. Fischer was not able to find the holotype of *psilocerus* in the Vienna Museum, where it ought to be preserved. However, the species can be recognized by details in Kohl's original description: head and thorax largely red, wings darkened mesally, propodeal hindface punctured, and tergum I not fasciate apically. No other *Tachysphex* has this combination of characters.

GEOGRAPHIC DISTRIBUTION (Fig. 104).—Mexico to Wyoming, east to Arkansas, west to eastern Arizona.

RECORDS AND MATERIAL EXAMINED.—UNITED STATES: ARIZONA: **Cochise:** 1 mi E Apache (1♀, AMNH), Portal (1♀, HKT), Sunnyside Canyon in Huachuca Mts. (1♀, UCD). ARKANSAS: **Newton:** —(1♀, UAF). COLORADO: **Boulder:** Boulder (holotype ♀ of *helianthi*, USNM; 1♀, CNC). **Larimer:** Chimney Rock 60 mi NW Fort Collins (1♀, CAS), Park Creek 20 mi N Fort Collins (1♂, WJP), Poudre Canyon (1♂, CU). TEXAS: **Presidio:** Marfa (1♀, NYSU). WYOMING: **Fremont:** Shoshone (1♂, UCD).

MEXICO: **Baja California Sur:** La Paz (holotype ♀ and paratype ♂ of *nitelopteroides*, CAS). **Distrito Federal:** Chapultepec (Kohl 1884). **Durango:** 7 mi W Durango (1♀, CNC), Nombre de Díos (1♀, CIS). **México:** Teotihuacán pyramids (1♀, 1♂, MCZ). **Sonora:** 10 mi E Navojoa (1♂, UAT).

Tachysphex ashmeadii W. Fox

(Figures 105, 106)

Tachysphex Ashmeadii W. Fox, 1894*a*:509, ♀ (incorrect original spelling). ! Holotype: ♀, California: San Diego (ANSP)—Dalla Torre 1897:678 (as *ashmeadis*); Ashmead 1899:250; Cresson 1928:43; Strickland 1947:129; G. Bohart 1951: 950; Krombein 1967:392; Bohart and Menke 1976:272; Krombein 1979:1631; Rust et al. 1983:406; Elliott and Kurczewski 1985:295; Parks 1986:34; Kurczewski 1987:122

Tachysphex posterus W. Fox, 1894*a*:510, ♀. ! Holotype: ♀, Washington: no specific locality (ANSP). Synonymized by R. Bohart *in* Bohart and Menke 1976:272.—Dalla Torre 1897:684; Ashmead 1899:250; Cresson 1928:45; G. Bohart 1951: 952.

Tachysphex spinosus W. Fox, 1894*a*:511, ♀. ! Holotype: ♀, California: Los Angeles Co.: no specific locality (USNM). Synonymized by G. Bohart 1951:950.—Dalla Torre 1897:685; Ashmead 1899:250; Rust et al. 1983:406.

Tachysphex spissatus W. Fox, 1894*a*:514, ♂. ! Holotype: ♂, California: no specific locality (ANSP). Synonymized by G. Bohart 1951:950.—Dalla Torre 1897:685; Ashmead 1899:250 (as *pissatus*); Cresson 1928:46.

Larra rufipes Provancher, 1895:129, ♀. ! Holotype: ♀, California: Los Angeles (Laval Univ. Quebec). Nec *Larra rufipes* (F. Smith, 1858) Kohl, 1885. Nec *Tachysphex rufipes* (Aichinger, 1870) Kohl, 1885. Synonymized by G. Bohart 1951:950

Tachysphex propinquus Viereck, 1904:87, ♀. ! Holotype: ♀, Arizona: Pinal Co.: Florence (ANSP). Synonymized by Pulawski *in* Krombein 1979:1632.—Snow 1906:8; Viereck 1906:235; Williams 1914:162, 202; Mickel 1918:425; Cresson 1928:45; G. Bohart 1951:962; Krombein 1961:82, 1967:393; Alcock and Gamboa 1975:164; Bohart and Menke 1976:276.

DIAGNOSIS.—*Tachysphex ashmeadii* can be recognized by its distinctive clypeus (Fig. 105a–c, f), the labrum convex and protruding in nearly all specimens (Fig. 105b, c), and the radially oriented midscutal setae that form a rosettelike pattern (Fig. 105d, e). In the other North American species the labrum is flat, usually concealed, and the scutal setae do not form a rosette (except in most *opata*, some *crassiformis*, some *pinal*, and some *yolo*). Other features of *ashmeadii* are: the basal platform of sternum II is angulate, the free margin of the male clypeus is shallowly concave between the lobe and orbit, and male sterna III–VI have well-defined graduli that delimit a triangular, basomedian area (*opata* lacks these three features). *Tachysphex ashmeadii* lacks a flat, horizontal depression at the apex of sternum I found in *yolo*. The clypeal lobe of *crassiformis* and *pinal* is markedly broader than in *ashmeadii*, and most *crassiformis* have an expanded or steplike axilla (see that species).

DESCRIPTION.—Galea and labrum variable (see Variation below). Clypeal free margin shallowly concave between lobe and orbit; middle section convex; bevel usually longer than basomedian area, but occasionally as long as the latter. Propodeal dorsum microareolate. Hindcoxa not carinate.

Middle scutal setae arranged in an oval, rosettelike pattern (Fig. 105d, e); setae oriented anterolaterad before center (anterad on middle), and posterad behind center.

Gastral terga I–IV silvery fasciate apically. Wings hyaline.

♀.—Clypeus (Fig. 105a–c): lip usually biarcuate, but occasionally evenly arcuate, not incised laterally. Dorsal length of flagellomere I 1.9–2.4× apical width. Vertex width 0.8–1.2× length. Punctures: on frons below midocellus mostly subcontiguous (but a few punctures usually about one diameter apart); on vertex less than one to about two diameters apart, usually fine, but sometimes relatively large; on scutum usually less than one diameter apart (mostly subcontiguous), but sometimes many discal punctures several diameters apart; on mesothoracic venter fine, less than one diameter apart; on trochanters and femora fine, subcontiguous. Mesopleuron microreticulate or finely punctate (punctures less than one diameter apart). Propodeal site microareolate, rarely microridged, occasionally punctate. Tergum V with dense or sparse punctures, its apical depression impunctate. Sterna III and IV with variously developed graduli. Pygidial plate punctate, interspaces smooth or alutaceous. Length 8.5–11.0 mm.

Setae appressed on vertex, except suberect or erect (0.75–1.0 MOD long) on postocellar depression, appressed on scutum and femora, partly obscuring mesopleural sculpture.

Color varying, but usually head, thorax, coxae, trochanters, and forefemur black, while remaining legs and gaster red. Lightest specimens have red scapus, middle clypeal section, part of flagellum, thorax, gaster, and legs. Melanistic individuals have black head, thorax, legs, and gastral segments V and VI or terga III and IV. All femora and tibiae black except femur partly red in a female from Temixco, Mexico (UCD).

♂.—Mandibular inner margin with obtuse tooth (Fig. 105f). Clypeus (Fig. 105f): lip evenly arcuate, its corners obtuse, closer to orbit than to each other. Dorsal length of flagellomere I 1.0–1.3× apical width, usually much less than flagellomere II. Vertex width 1.2–1.4× length. Punctures on frons below midocellus subcontiguous to about one diameter apart; on vertex fine to relatively large, less than one diameter apart; on scutum well defined, mostly (except small specimens) more than one diameter apart on each side of midline; on mesopleuron variable (see below). Propodeal side microareolate, microridged, or punctate (interspaces microsculptured). Tergum VII flattened, densely punctate. Sterna densely punctate and pubescent, sterna III–VI with graduli. Forefemoral notch variable. Outer margin of forebasitarsus usually without preapical spines, occasionally with one or two preapical spines; apical spine longer or shorter than basitarsal width. Length 5.5–8.5 mm.

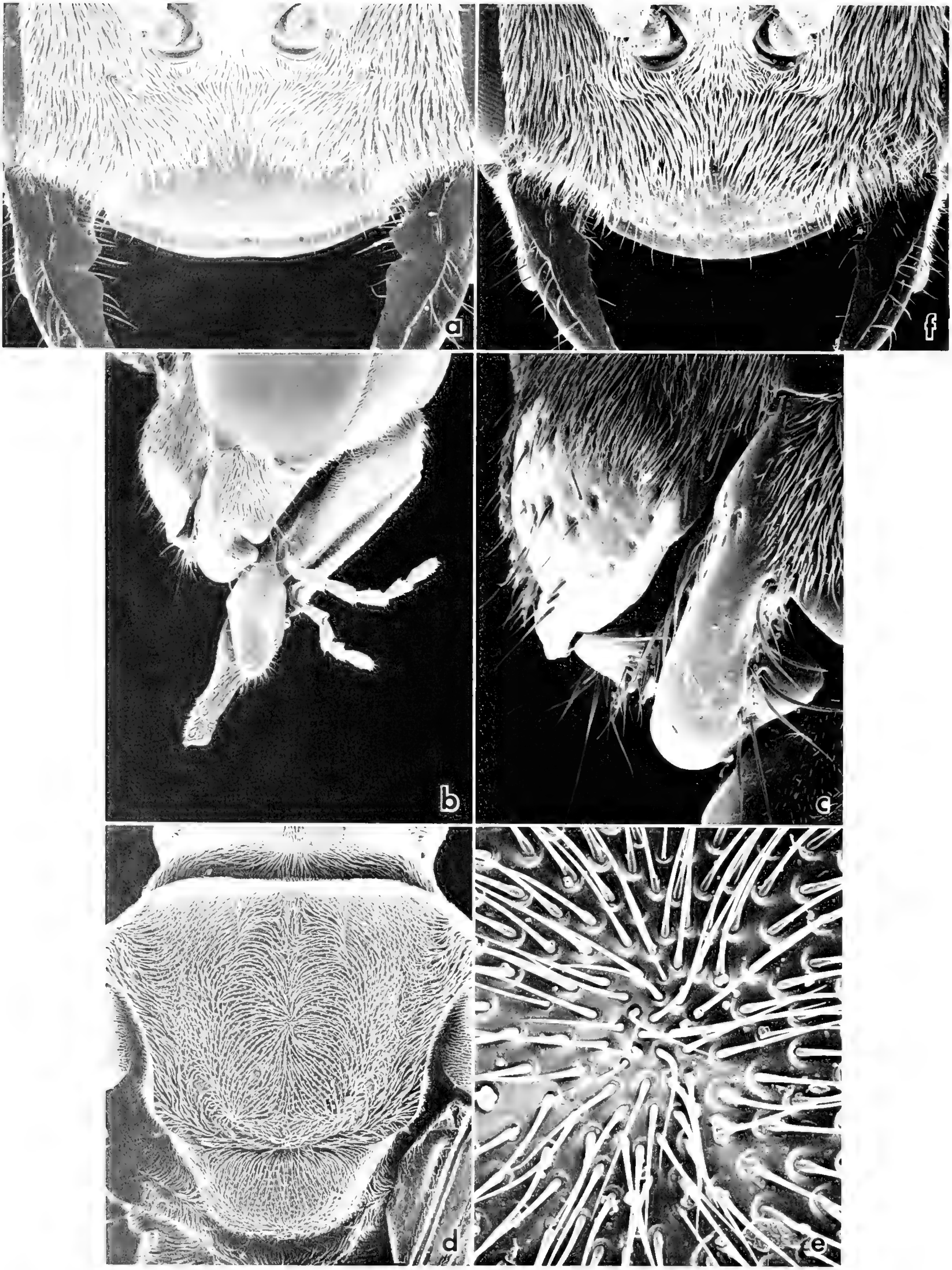

FIGURE 108. *Tachysphex ashmeadii* W. Fox: a—female clypeus, b—lower part of female head, laterally; c—female clypeus, labrum and mandible; d—female scutum and scutellum, e—midscutal setae of female, f—male clypeus.

Setae appressed to erect, 0.75–1.0 MOD long on vertex, 1.0–1.25 MOD long on scutum; appressed on midfemoral venter.

Head and thorax black. Gastral segments I and II to I–IV red, remainder black; rarely all sterna black, and gaster all black in a male from Pyramid Lake, Nevada (UCD). Legs black. Frontal vestiture silvery.

VARIATION.—In most specimens, the labrum is convex, protruding beyond the clypeal free margin, and the galea is about as long as wide (Fig. 105b, c). However, these structures are relatively short in some Californian specimens, and occasionally the labrum is nearly flat and does not exceed the clypeal margin, and the galea is shorter than wide.

The frontal and thoracic vestiture is silvery in most specimens, but has a golden tinge in some Mexican females (Guerrero: Zumpango; Morales: Temixco; Puebla: Petlalcingo; Sinaloa: Elota, Mazatlán; 6♀, UCD).

Sculpture and vestiture vary in males and the extreme forms are characterized as follows:

1) Mesopleural punctures fine, subcontiguous; propodeal side dull, with abundant microsculpture, punctures evanescent; setae appressed on vertex and scutum, about 0.75 MOD long on vertex; erect microsetae of antennal flagellum very short.

2) Mesopleural punctures large ventrally, one to three diameters apart; propodeal side shiny, with well-defined punctures. Microsculpture evanescent; setae erect on vertex and scutum, about 1.0 MOD long on vertex; erect microsetae of antennal flagellum relatively long.

These two extremes, as well as intermediate forms, have been found at Hasty, Colorado; La Joya, New Mexico; Nixon, Nevada; and in many other localities.

DISCUSSION.—The relationship of *ashmeadii* to other species in the genus is somewhat unclear. Generally *ashmeadii* resembles the Old World *panzeri* group and the Neotropical *undatus* group in having a convex, protruding labrum (labrum flat in some small *ashmeadii*), and a slightly elongate galea. However, the shape of the galea, the presence of well-defined graduli on male sterna III–VI, and the geographic distribution (western North America), suggest that *ashmeadii* is unrelated to these groups. Characters of the *panzeri* group are: the galea is longer than wide (in *ashmeadii*, about as long as wide or wider), length of male vertex 0.5–1.1 × width (1.2–1.4 in *ashmeadii*), and male sterna lack graduli. In the *undatus* group, the galea is longer than wide, the propodeal sculpture is coarser than in *ashmeadii*, especially on the dorsum, and male sterna also lack graduli. The vertex setae are appressed or nearly so in the *panzeri* group, erect in the *undatus* group, and either appressed or erect in *ashmeadii*. Most probably *ashmeadii* is an aberrant member of the *pompiliformis* group, close to such species as *amplus*, *lamellatus*, *sonorensis*, *texanus*, and *yolo*. These species resemble *ashmeadii* in details of sculpture and vestiture, and their labrum may be slightly prominent (although it is generally flat).

LIFE HISTORY.—Males and females from the Apache and Portal area, Arizona, were collected on flowers of *Baccharis glutinosa* Pers., and specimens from Antioch, California, were collected on flowers of *Croton californicus* Muell.-Arg. and *Eriogonum nudum* (Dougl. ex Benth.). A female from Logan, Utah (USU), was captured on flowers of *Daucus carota* L. Nesting takes place in sandy soils. Nest digging may start either from the surface or from preexisting depressions such as animal tracks (Elliott and Kurczewski 1985). Digging females enter the burrow headfirst and throw sand backward with forelegs (which work in unison) while backing out from the burrow. The nest is unicellular and permanently open during the provisioning period. The tumulus that accumulates during digging is left intact. The nest's length and depth vary: the nests observed by Williams (1914) were 5.0–7.5 cm long and ended 2.5–5.0 cm below the surface, those observed by Elliott and Kurczewski (1985) were 8.9–10.4 cm and 5.0–5.9 cm, respectively, while Kurczewski (1987) reported 3.5 and 1.5 cm. Completion of the nest is followed by an orientation flight. Recorded prey are nymphs and adults of Acrididae as listed below:

Species	Source
Ageneotettix deorum (Scudder)	Williams 1914; Lavigne and Pfadt 1966
Arphia sp.	Elliott and Kurczewski 1985
Bruneria sordida (McNeill)	Elliott and Kurczewski 1985
Cordillacris crenulata (Bruner)	Williams 1914; Krombein 1979
Cordillacris occipitalis (Thomas)	Lavigne and Pfadt 1966
Melanoplus bivittatus (Say)?	Elliott and Kurczewski 1985
Melanoplus lakinus Scudder	Elliott and Kurczewski 1985
Melanoplus sanguineus (Fabricius)	Elliott and Kurczewski 1985
Melanoplus sp.	Elliott and Kurczewski 1985; Kurczewski 1987
Metator sp.	Krombein 1967
Opeia sp.	Krombein 1967
Orphulella sp.	Elliott and Kurczewski 1985
Philibostroma sp.	Krombein 1967
Trachyrhachis kiowa (Thomas)	Williams 1914; Lavigne and Pfadt 1966
Trimerotropis bilobata Rehn and Hebard	Elliott and Kurczewski 1985
Trimerotropis pallidipennis (Burmeister)	Elliott and Kurczewski 1985
Trimerotropis sp	Elliott and Kurczewski 1985

In addition, I have seen females pinned with prey not previously reported (prey identification by D. C. F. Rentz when not indicated otherwise). They are listed below:

Species	Locality and depository
Aulocara sp.	Oklahoma: Lake Texoma (UCD)
Dissosteira pictipennis Bruner	California: Arroyo Seco (UCD)
Cordillacris occipitalis (Thomas)	California: Cajon (UCD)
Orphulella pelidna (Burmeister)	Texas: Padre Island (CAS, det. D. Otte)
Schistocerca sp	Oklahoma: Lake Texoma (UCD)
Trimerotropis sp.	Arizona 3 mi E Portal (CAS)

The prey are often much larger than the wasp, and prey's head is sometimes masticated by the wasp to obtain liquids (Williams 1914). Prey are transported (Williams 1914; Kurczewski 1987) on the ground and/or in short flights, but small prey are carried exclusively in flight (Williams 1914). His description suggests that the prey were kept venter up. They are held by the bases of their antennae with the wasp's mandibles. Prey are taken into the nest without stopping at the entrance and deposited in the cell head inward and in most cases venter up; Alcock and Gamboa (1975) and Kurczewski (1987) found one prey positioned on its side. Most cells contain a single prey, but Elliott and Kurczewski (1985) found two cells, each with two prey, in Saint Anthony, Idaho. In the single case examined, the egg was laid on the grasshopper brought last into the nest. Kurczewski (1987) reported that the egg was laid on the left forecoxal corium and extended transversely between the fore- and midcoxae.

GEOGRAPHIC DISTRIBUTION (Fig. 106).—Xeric areas west of the 95th meridian, north to southern Canada, south to Costa Rica; also Florida panhandle.

FIGURE 106. Geographic distribution of *Tachysphex ashmeadii* W. Fox.

MATERIAL EXAMINED.—2,022♀, 1,775♂.

RECORDS.—CANADA: **Alberta:** Medicine Hat, 12 km SW Orion, Writing-on-Stone Provincial Park. **British Columbia:** Osoyoos.

UNITED STATES: ARIZONA: **Apache:** Canyon de Chelly, Chinle. **Cochise. Coconino. Gila:** 3 mi SW Christmas, San Carlos, 5 mi N Seneca. **Graham. Maricopa. Mohave. Navajo. Pima. Pinal. Santa Cruz. Yavapai. Yuma.** CALIFORNIA: **Alameda:** Livermore (also 15 mi E, 17 and 20 mi S), Sycamore Grove State Park. **Butte:** Chico. **Colusa:** Ladoga. **Contra Costa:** Antioch. **El Dorado:** Chili Bar, 10 mi NE on Ice House road. **Fresno. Glenn:** Artois. **Humboldt:** Honeydew. **Imperial. Inyo. Kern. Lassen:** Hallelujah Junction, 2.9 mi E Susanville. **Los Angeles. Mariposa:** 2 mi S Mormon Bar. **Mendocino:** Navarro River at Highway 128 (Hendy Grove State Park), Twin Rocks (5 air mi E Cummings). **Modoc:** Alturas (also 3 mi W and 10 mi N). **Mono. Monterey. Nevada:** Boca, Nevada City, Sagehen Creek near Hobart Mills. **Orange:** Corona del Mar, Costa Mesa, Santa Ana. **Placer:** Auburn. **Plumas. Riverside. Sacramento. San Benito. San Bernardino. San Diego. San Joaquin:** Corral Hollow (8 mi SW Tracy). **San Luis Obispo. Santa Barbara. Santa Clara:** San Antonio Ranger Station. **Santa Cruz:** Mt. Hermon, Watsonville. **Shasta:** Hat Creek Post Office, Redding. **Siskiyou. Solano:** Rio Vista. **Sonoma:** Geyserville. **Stanislaus:** Del Puerto Canyon, Patterson (also 5 mi W). **Tehama:** Manton, Red Bluff. **Trinity:** Junction City. **Tulare:** Lemon Cove, Three Rivers. **Tuolumne:** Brown Meadow, Groveland, Strawberry. **Ventura. Yolo:** Davis, Rumsey. COLORADO: **Bent:** 2 mi S Hasty. **Boulder:** White Rock near Boulder. **Crowley:** Crowley. **Larimer:** Fort Collins. **Mesa:** Colorado National Monument. **Moffat:** Sunbeam. **Montezuma:** Mancos River (28 mi S Cortez). **Morgan:** 6 mi E Wiggins. **Prowers:** Carlton, 13 mi S Lamar. **Sedgwick:** Julesburg. **Weld:** Roggen. FLORIDA **Okaloosa:** Destin (1♂, FSCA). IDAHO: **Ada:** Boise. **Bingham:** 6 mi NW Aberdeen. **Blaine:** Carey. **Boise:** 1 mi W Horseshoe Bend. **Bonneville:** 5 mi W Idaho Falls. **Canyon:** Marsing, 2 mi N Melba, Nampa, Parma. **Cassia:** 5 mi SE Malta (also 9 mi E), Yale. **Elmore:** 1 mi W Glenns, Hammett, 13 mi S Sunnyside. **Franklin:** Preston (also 3 mi NW). **Fremont:** Saint Anthony Sand Dunes. **Gooding:** 5 mi N Bliss, 1 mi NE Gooding (also 3 mi S), Hagerman Valley. **Lincoln:** 5 mi E Dietrich, 7 and 9 mi W Shoshone. **Minidoka:** Acequia. **Oneida:** 5 mi S Holbrook, Rock Creek. **Owyhee. Twin Falls.** KANSAS: **Clark, Graham, Grant, Greeley, Morton, Phillips, Seward, Stevens:** —. **Kearny:** Lakin, McKinney Lake. **Wallace:** Sharon Springs. MONTANA: **Stillwater:** —. NEBRASKA: **Box Butte:** Alliance. **Cherry:** Valentine Lakes Refuge. **Dawes:** Chadron. **Dawson:** Cozad. **Lincoln:** Wallace. **Sheridan:** Rushville. **Sioux:** Harrison. **Thomas:** Dismal River in Bessy National Forest, Halsey, Thedford. NEVADA: **Carson City:** Carson City. **Churchill:** Eastgate (also 6 mi SE), Fallon (also 5 mi NE and 23 mi E), 3 mi W Hazen. **Clark. Douglas:** 3 mi S Genoa, 3 mi N Minden, Topaz Lake. **Elko:** 6 mi S Deeth. **Esmeralda:** 15 mi S Goldfield. **Eureka:** Beowawe Pass, Emigrant Pass, Eureka. **Humboldt. Lander:** 5 mi W Austin. **Lincoln. Lyon. Mineral. Nye. Pershing:** Woolsey. **Storey:** Geiger Gd. **Washoe. White Pine:** Spring Valley. NEW MEXICO: **Bernalillo:** Albuquerque. **Catron:** Pie Town. **Cibola:** Acoma Pueblo, 5 mi E Laguna. **Dona Ana:** Hatch, Las Cruces (also 12 mi SW, 19 mi W), Leasburg Dam State Park. **Grant:** Hurley, 14 mi NW Silver City. **Guadalupe:** Santa Rosa. **Hidalgo. Lea:** 2 mi NW Tatum. **Lincoln:** Nogal. **Luna:** Columbus, 6 mi NW Florida. **Otero:** 35 mi NE Las Cruces, White Sands National Monument. **Quay:** Tucumcari, Ute Lake. **Sandoval:** Jemez Springs. **Sierra:** Percha Dam State Park. **Socorro. Torrance:** Gran Quivira (town). OKLAHOMA: **Marshall:** Lake Texoma (2 mi E Willis). OREGON: **Grant:** Dixie. **Harney:** Roux Creek (3 mi S 2 mi W Fields). **Malheur:** 6 mi E Burns Junction, Jordan Valley (also 50 mi W). **Umatilla:** Hat Rock State Park. TEXAS: **Bastrop:** 6 mi E Bastrop, McDade. **Bexar:** —. **Brazos:** College Station, Wellborn. **Brewster. Brooks:** Encino (also 8 mi E), Falfurrias. **Cameron:** 14 mi E Brownsville. **Crockett:** Fort Lancaster Historical State Park. **Culberson:** Plateau, Van Horn. **El Paso:** El Paso (also 15 mi E). **Guadalupe:** Seguin. **Harrison:** 2 mi S Waskom. **Hidalgo:** McAllen Botanical Garden. **Hudspeth. Jeff Davis:** 10 mi W Fort Davis. **Jim Hogg:** 3 mi SW Hebbronville. **Jim Wells:** Palito Blanco. **Karnes:** Guillette. **Kleberg:** Kingsville (also 20 mi SE), Riviera. **Lee:** Fedor, Giddings. **Maverick:** Quemado. **Mitchell:** Lake Colorado City State Park. **Nueces:** Padre Island. **Presidio:** Marfa (also 8 mi E), 2 mi E Presidio. **Somervell:** Dinosaur Valley State Park. **Tarrant:** Colleyville. **Ward:** 1 mi S Grandfalls, 8 mi E Monahans. **Webb:** 15 mi SE Laredo (also 32 air mi N). **Zapata:** Falcon State Park, San Ygnacio. UTAH: **Box Elder. Cache:** Cornish, Logan. **Emery. Garfield. Grand:** Canyonland National Park, Salt Valley (NW Arches National Park). **Juab:** White Sand Dunes (25 mi SW Eureka). **Kane:** 23 mi N Page (in Arizona). **Millard. Uintah:** SW Bonanza. **Utah:** Utah Lake. **Washington. Wayne:** Hanksville. WASHINGTON: **Benton:** Riverland. **Franklin:** 28 mi S Othello. **Grant:** O'Sullivan Dam, Stratford. **Whitman:** Wawawai. **Yakima:** 5.5 mi S Toppenish, Yakima City. WYOMING: **Converse:** Glenrock. **Fremont:** Shoshoni. **Natrona:** Powder River. **Platte:** Glendo. **Sweetwater:** Wamsutter. **Washakie:** Worland.

MEXICO: **Baja California Norte. Baja California Sur. Chihuahua:** 10 and 20 mi N and 15 mi S Chihuahua, 4 mi N Ciudad Camargo, 5 mi N Escalon, Hidalgo del Parral (also 9 mi S), 60 mi S Juárez, Moctezuma, 10 km S Villa Ahumada. **Coahuila:** 10 km SW Cuatrociénegas, 61 mi N Saltillo. **Colima:** Manzanillo. **Durango:** 4 mi N Nombre de Dios. **Guerrero:** Xalitla, Zumpango. **Jalisco:** Chamela, El Tuito, Plan de Barrancas, Playa Cuitzmala 8 km S Careyes. **Morelos:** 3 mi N Alpuyeca, 6 mi S Temixco, 7.3 mi S Yautepec. **Nayarit:** San Blas. **Oaxaca:** 3 mi W Camarón, 12 mi S Chivela, 23 mi S Mathias Romero, 3 mi E Salina Cruz, Tehuantepec. **Puebla:** Petlalcingo. **Sinaloa:** 6 mi NW Choix, Elota (also SE), 28 km N Los Mochis, Mazatlán, San Lorenzo, 21 mi E Villa Unión. **Sonora:** Alamos (also 10 mi SE), Cócorit, Desemboque, Guaymas, Hermosillo, 10 mi E Navojoa, San Carlos (also 6 km NNW), 32 mi SW Sonoita. **Tamaulipas:** Jaumave (road 101 W Ciudad Victoria), Matamoros (also 30 mi SE), Playa Altamira. **Veracruz:** Tecolutla (also 16 mi S), Veracruz. **Zacatecas:** 9 mi S Fresnillo, 9 mi N Ojocaliente.

CENTRAL AMERICA: COSTA RICA: Junquillal Beach. EL SALVADOR: Playa Icacaya (30 km SW Unión).

terminatus Species Group

Members of the *terminatus* group are defined by the presence of a callosity behind each hindocellus (Fig. 114a); in addition, the labrum is flat, the tarsomeres are not modified, and the setae of the propodeal dorsum are oriented toward the thorax. The callosities are also found in two species belonging to other groups, *iridipennis* (*brullii* group) and the South American *apoctenus* Pulawski (*undatus* group). However, propodeal setae are inclined toward the gaster and the female tarsi are modified in *iridipennis*, and the labrum is convex in *apoctenus*. The common color pattern in the group is a black body with a red gastral tip. In other New World *Tachysphex*, this pattern is found only in *alayoi*, *toltec*, and in some *cubanus*.

Prey consists mainly of Acrididae, but *terminatus* rarely uses Tettigoniidae.

The group is widespread in the New World, ranging from about 63°N in Alaska to about 40°S in Argentina. Of the 11 known species, six are found in North America, *ruficaudis* ranges between southern United States and Argentina, *antillarum* and *quisqueyus* occur in the West Indies, *galapagensis* Rohwer in the Galapagos Islands, and *peruanus* Pulawski on the Peruvian coast (Pulawski 1986).

Characters shared by all species of the *terminatus* group are: clypeal bevel shorter than basomedian area, evanescent in some specimens; vertex width more than length or slightly less; scutal hindcorners rounded (*clarconis*, *galapagensis*) or weakly prominent; mesothoracic venter densely punctate; propodeal side ridged (except unridged in most *galapagensis* and some small males of other species); male sterna III–VI with graduli; vestiture not obscuring sculpture on gena, thorax, and femora; vertex setae erect; scutal setae erect or inclined backwards but not appressed, at least 0.5 MOD long; setae of midfemoral venter 0.3–1.0 MOD long; head, thorax, and legs black.

Unlike the other groups treated here, cladistic analyses were performed on members of the *terminatus* group because: (1) its monophyly is convincingly demonstrated by the presence of a unique synapomorphy, the postocellar swellings (I regard the swellings in *apoctenus* and *iridipennis* as a convergence), and (2) it was possible to take all 11 known members into consideration (by including two extralimital species, *galapagensis* and *peruanus*). Sixteen morphological and biological characters were used in the analyses. Transformation series and character polarities were established by outgroup comparison. Other *Tachysphex* were selected as the principal outgroup, but other Tachytina were also considered. Character states and transformation

series are as follows (the letter a indicates the plesiotypic condition, the letters b–g various apotypic conditions):

1) *Frons sculpture.* The frons is variously sculptured in Larrinae, and I regard as primitive a uniformly microsculptured, dull integument with dense, inconspicuous punctures. Within the *terminatus* group, I consider the densely punctate frons with microsculptured interspaces (a) as plesiotypic, and as apotypic the microrugose frons (b) of *similis,* the punctatorugose or rugose frons (c) of *ruficaudis,* and the shiny frons (d) of *apicalis,* with b, c, and d deriving independently from a.

2) *Clypeal width to length ratio.* I regard as plesiotypic, in the *terminatus* group, a medium wide clypeus (a), with the width to length ratio 2.8–3.2 in the female and 3.1–3.3 in the male (or nearly so). I regard as apotypic both a narrow (b) and a broad clypeus (c). The clypeus is narrow if the ratio is 2.0–2.8 in the female and 2.1–2.7 in the male, and broad if the ratio is 3.0–3.4 in the female and 3.2–3.6 in the male.

3) *Clypeal lip of female.* The clypeal lip of the female is plesiotypic if evenly arcuate (a), and apotypic if broadened or produced mesally (b).

4) *Clypeal lip of male.* The clypeal lip is straight, arcuate, or sinuate (a) in most species, but triangular (b) in *peruanus.*

5) *Inner mandibular margin of male.* In most species, the male mandible has a tooth on the inner margin (a), but it is toothless (b) in *peruanus.*

6) *Width of female vertex.* The vertex is narrow (a) in *galapagensis, peruanus,* and *similis* (width 1.3–1.7 × length), and broad (b) in the remaining species (width 1.7–2.6 × length).

7) *Mesopleural punctures.* The mesopleuron is variously sculptured in Larrinae; an impunctate, uniformly microsculptured mesopleuron is probably plesiotypic. I accept that, in the *terminatus* group, the shallow, ill-defined but uniformly dense punctures (a) found in the female of *galapagensis* are plesiotypic, that the well-defined punctures (b) of other species derived from a, and that the well-defined, sparse punctures (c) of *ruficaudis* derived from b.

8) *Metapleural flange.* The metapleural flange is narrow, inconspicuous (a) in most Larrinae, but expanded (b) in some, including most species of the *terminatus* group.

9) *Oblique carina beneath anterior end of metapleural flange.* This carina is absent (a) in most Larrinae, but rudimentary (b) in *antillarum* and well developed (c) in most other members of the *terminatus* group. It attains the external margin of the flange (d) in most *linsleyi.* I assume a linear transformation series.

10) *Prespiracular prominence of upper metapleuron.* The upper metapleuron is simple (a) in the vast majority of Larrinae. It has a short carina before the propodeal spiracle (b) in *antillarum,* and a long carina, extending to the anterior end of the flange (c) in *ruficaudis* (the long carina has probably evolved from b). A low prominence, obtusely angulate in side view (d), found in *alpestris,* has probably also derived from b. The funnel-shaped prominence unique to *linsleyi* (e), and a tall, broad prominence (f) found in *apicalis, quisqueyus,* and *terminatus* have probably developed from d. A tall, sharp prominence (g) found in most *similis* has probably derived from f.

11) *Sculpture of propodeal side.* This area is variously sculptured in Larrinae, but a uniformly microsculptured integument is probably plesiotypic. I accept that the nonridged (or weakly ridged) propodeal side of *galapagensis* is plesiotypic (a), and that a distinctly ridged propodeal side of other species derived from a.

12) *Basal tooth of hindcoxa.* The tooth is absent in many *Tachysphex* and other larrine genera, and low (a) or high (b) in members of the *terminatus* group.

13) *Male forefemoral notch.* In most Larrinae the forefemur is entire. Within *Tachysphex* a notched forefemur (a) is plesiotypic, because it occurs in most species of the genus, including the least specialized ones. The entire forefemur (b) of some *Tachysphex* is a reversal, because it occurs in evidently unrelated species, none of which is morphologically primitive.

14) *Male foretarsal rake.* I regard the rake's absence (a) as plesiotypic in the genus and its presence (b) as apotypic.

15) *Vertex setae.* I regard short setae as plesiotypic, because this type occurs in the least specialized members of the genus (such as *pompiliformis*). Within the *terminatus* group, the vertex setae are either short (a): less than 2.0 MOD in the female; or long (b): 2.0 MOD or more in the female.

16) *Nest placement.* Most Larrini nest in both flat or inclined ground (a), but *apicalis* establishes its nests exclusively in sloping banks or cliffs (b). The nesting habits have not been observed in *antillarum, galapagensis, peruanus,* and *quisqueyus,* and I accept for the purpose of this analysis that they nidify in flat ground.

The above list includes 27 character states. Four characters (1, 4, 5, and 16) are autapomorphies and thus have no value in establishing relationships between species.

Two microcomputer packages were used to infer phylogenetic relationships: CLINCH Version 6.2 (Kent Fiala's compatibility program) and PAUP Version 2.4 (David Swofford's parsimony package).

The CLINCH algorithm found that 11 was the maximum number of compatible characters. There were two groups (cliques) of such characters. The first consisted of characters 7, 8, 9, 11, 12, 13, and 15 (plus the autapomorphies), the second of characters 2, 7, 8, 9, 10, 11, and 12. I preferred the second clique because it contained character 10 (metapleural carinae and prominences), unusual in *Tachysphex,* rather than character 15 (length of vertex setae), which is plastic within the genus. A secondary compatibility analysis was performed on the portion of the cladogram not resolved in the primary analysis. Incompatible characters were then manually added to the cladogram, and its length was minimized by accepting reversals of character 6 in *similis,* and of character 15 in *apicalis* and *ruficaudis.* The cladogram length was 36 steps (transformations).

The PAUP branch and bound algorithm found that 36 steps was the minimum cladogram length. It generated 117 cladograms of that length, although many were topologically identical (an unresolved trichotomy is treated by the algorithm as three sets of two successive dichotomies with one zero-length branch). One of the cladograms, common to both the compatibility and parsimony analyses, was accepted (Fig. 107).

All cladograms were in consensus that: (1) *galapagensis* is the most primitive member of the group, identical to the group's ancestor (this conclusion is correct only if the polarity accepted for characters 7 and 11 is correct); (2) *peruanus* is a sister species of all remaining species, and not an ancestor of *galapagensis,* as the geographic distribution of these species may suggest (*peruanus* apparently evolved from the group's ancestor, whereas

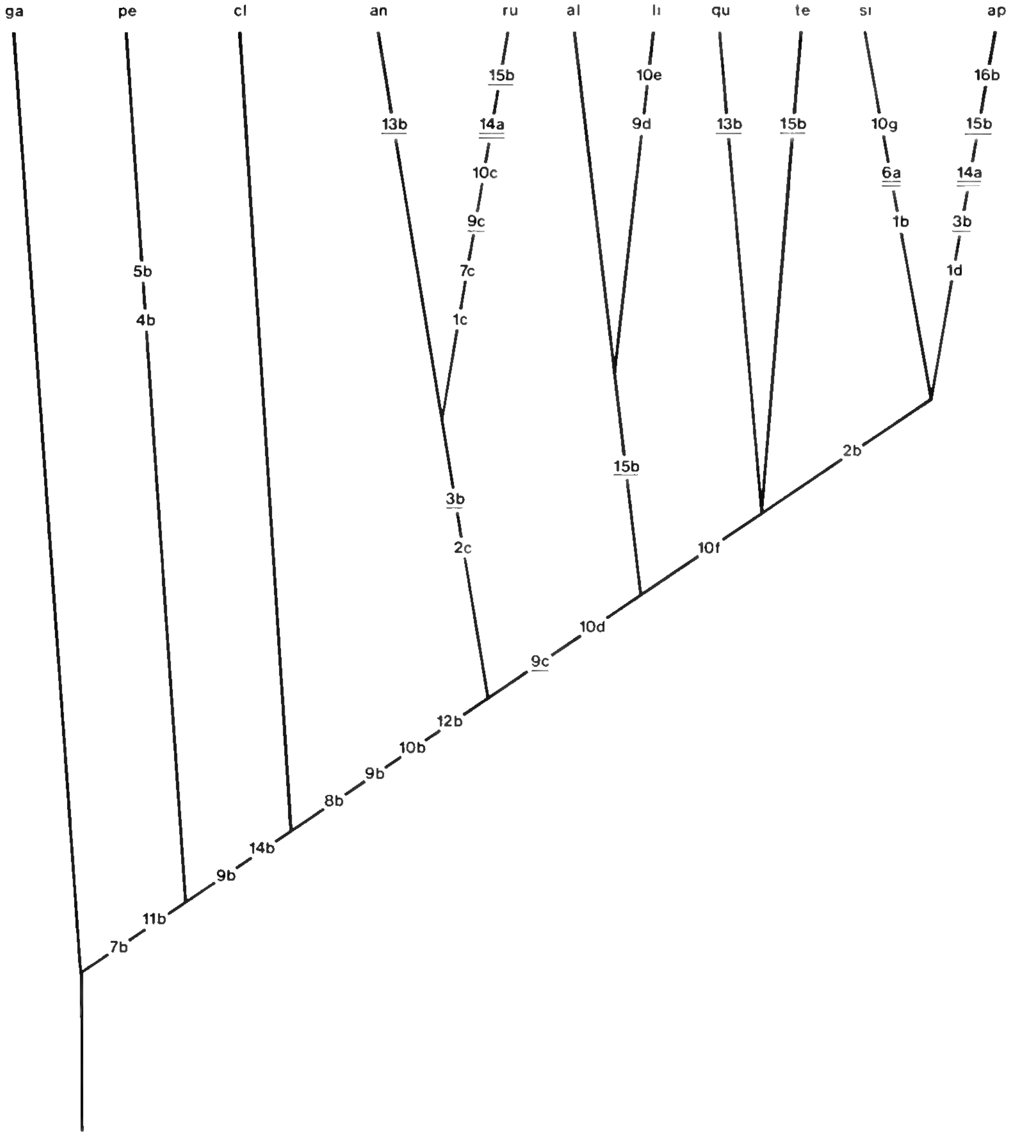

FIGURE 107. Hypothetical phylogenetic tree of all known members of the *terminatus* group. Numbers and letters refer to the characters listed in the text (plesiomorphic states are omitted); underlining indicates parallelisms, and double underlining indicates reversals; al—*alpestris*, an—*antillarum*, ap—*apicalis*, cl—*clarconis*, ga—*galapagensis*, li—*linsleyi*, pe—*peruanus*, qu—*quisqueyus*, ru—*ruficaudis*, si—*similis*, te—*terminatus*

galapagensis retained its plesiotypic characters); (3) *clarconis* is the sister group of all other members of the group excluding *galapagensis* and *peruanus*; and (4) the monophyly of the remaining eight species is strongly supported by four synapomorphies (8b, 9b, 10b, 12b).

All cladograms also suggested multiple parallelisms and reversals during the group's evolution. The cladogram in Figure 107 suggests that: (1) character 3b (clypeal lip of the female with a median projection) developed in the common ancestor of *antillarum* and *ruficaudis*, and also in *apicalis*; (2) character 9c (oblique metapleural carina) evolved in *ruficaudis* and also in the common ancestor of six terminal species; (3) character 12b (entire male forefemur) appeared independently in *antillarum* and *quisqueyus*; and (4) character 14b (long vertex setae) was acquired by the common ancestor of *alpestris* and *linsleyi*, and also by *terminatus*. The cladogram also suggests the following reversals: (1) a secondary narrowing of the vertex (character 6) in *similis*; and (2) a secondary loss of the foretarsal rake (character 14) in the males of *apicalis* and *ruficaudis*.

Tachysphex clarconis Viereck

(Figure 108)

Tachysphex clarconis Viereck, 1906:211, ♀, ! Holotype: ♀, Kansas: Clark Co., no specific locality (KU).—Williams 1914:173, G. Bohart 1951:950, LaBerge 1956:527, Bohart and Menke 1976:273, Krombein 1979:1631, Elliott and Kurczewski 1985:294, Rust et al. 1985:46, 53.

Tachysphex plesia Rohwer, 1917*b*:245, ♀ (wrong gender ending, *plesius* is correct). ! Holotype: ♀, California: El Dorado Co.: Tahoe (USNM). Synonymized by Pulawski *in* Krombein 1979:1631.—G. Bohart 1951:952, Bohart and Menke 1976:275

Tachysphex sp. near *linsleyi*: Evans 1970:490, corrected to *Tachysphex clarconis* by Kurczewski and Evans 1986:720

DIAGNOSIS.—*Tachysphex clarconis* differs from other North American members of the *terminatus* group in having an unspecialized metapleuron: its upper portion is ridged but has neither a prominence before the propodeal spiracle nor an oblique carina beneath the anterior end of the flange (there may be a rudimentary ridge there); and the flange is narrow. Unlike most species of the group, the gaster is all red in most females and many males of *clarconis* (and also in certain populations of *alpestris* and *linsleyi*).

The postocellar callosities are indistinct in some males, but males can be recognized by the well-developed foretarsal rake combined with broad vertex (width more than twice length).

The upper metapleuron is identical in *clarconis, galapagensis,* and *peruanus,* but in the latter two the vertex width is 1.3–1.5 (female) and 1.6–1.7× (male) length, the foretarsal rake is rudimentary or absent, the propodeal side of *galapagensis* is not ridged or indistinctly ridged, the female mesopleuron of *galapagensis* is indistinctly punctate, the male clypeus of *peruanus* is triangular, and its mandible is not dentate on the inner margin.

DESCRIPTION.—Scutal punctures no more than one diameter apart in some black males, but in most specimens punctures less than one diameter apart adjacent to margins and around admedian lines and two or three to several diameters apart in remaining U-shaped area. Metapleural flange narrow. Upper metapleuron with a few simple, longitudinal ridges before propodeal spiracle, at most with rudimentary, oblique ridge beneath anterior end of flange. Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa low, obtuse.

Vestiture not obscuring or partly obscuring sculpture between antennal socket and orbit.

Gaster red (except tergum I black basally) to all black; black except reddish apically in females from San Nicolas Island, California, and in a female from junction of Springs Road and Highway 97, California. Terga I–IV (I–V in male) silvery fasciate apically). Wings almost hyaline to moderately infumate.

♀.—Clypeal width 2.8–3.2× length; bevel shorter than basomedian area; lip arcuate, without mesal projection. Dorsal length of flagellomere I 1.7–1.9× apical width. Vertex width 1.9–2.2× length. Frons distinctly punctate to rugose. Length 6.0–7.5 mm.

Setal length about 1.7 MOD on vertex and about 1.3 MOD anterolaterally on scutum (about 1.6 in specimens from Needles and Palo Verde, California, from Willcox area, Arizona, and in some specimens from Tombstone area, Arizona).

♂.—Clypeal width 3.1–3.3× length; lip evenly arcuate to slightly sinuate; corners prominent but obtuse, closer to antennal socket than to each other or equidistant. Frons punctate to punctatorugose. Vertex width 2.1–2.6× length. Sterna pubescent throughout. Foretarsus with rake; outer apical spine of foretarsomere II longer than tarsomere III. Length 4.5–6.5 mm.

Setal length about 1.3–1.7 on vertex and about 1.0 MOD anterolaterally on scutum (but varying from 1.2 to 1.6 in black specimens from Needles, California, and about 1.7 in specimens from Willcox area, Arizona, and from Percha Dam State Park, New Mexico).

DISCUSSION.—The holotype female of *clarconis* differs from other specimens examined in having a finely punctate mesopleuron (most interspaces broader than punctures), evanescent ridges on the propodeal side, and the scutal setae 1.3 MOD long anterolaterally. Since no similar specimen has been found, and because other characters are identical, I regard the specimen as an individual variant, and therefore conspecific with other specimens studied, including the holotype of *plesius,* and the names *clarconis* and *plesius* as synonyms.

LIFE HISTORY.—Evans (1970) observed nesting habits of this species in Jackson Hole, Wyoming (as sp. near *linsleyi*), and Elliott and Kurczewski (1985) in St. Anthony, Idaho. Completion of the nest is followed by an orientation flight. The nest is temporarily closed when the wasp is hunting. The female walks with prey or, if the prey are small, she carries them in a series of short flights. They hold prey with their mandibles by the base of the antennae. Prey are nymphs of the acridids *Melanoplus foedus* Scudder, *Melanoplus sanguinipes* (Fabricius), and a third species which probably is *Chloealtis conspersa* (Harris). The female drops her prey near the nest entrance, opens it, enters, reappears headfirst, and pulls the grasshopper inside by its antennae. Three to six prey are stored per cell. The nest has one or two cells. The egg is deposited on a prey's prosternum, transversely behind the front coxae.

GEOGRAPHIC DISTRIBUTION (Fig. 108).—Rocky Mountains west to the Pacific Coast, from southwestern British Columbia to Baja California Norte and southern New Mexico, also Kansas.

MATERIAL EXAMINED.—637♀, 645♂.

RECORDS (b: gaster black).—CANADA: **British Columbia:** Comox (b).

UNITED STATES: ARIZONA: **Cochise:** 2 mi NE Portal, 14 mi W Tombstone, 3 mi E Willcox (also 4 mi S). **Maricopa:** Tempe. **Santa Cruz:** Sonoita. **Yavapai:** Cottonwood. CALIFORNIA: **Alameda:** Sycamore Grove Regional Park. **Alpine:** 1 mi E Carson Pass, Hope Valley, Red Lake. **Butte:** 20 mi NE Yuba City. **Contra Costa:** Antioch, Danville (b). **El Dorado** (partly b). **Fresno:** Fresno (also 25 mi E), Huntington Lake. **Glenn:** Plaskett Meadows. **Humboldt** (partly b). **Imperial:** Palo Verde (partly b). **Inyo:** Deep Springs, Little Lake, Westgard Pass. **Kern:** Dove, Piute Mts., Short Canyon. **Lassen:** Hallelujah Junction (partly b). **Los Angeles. Marin** (some b). **Mariposa:** Mariposa, Wawona. **Mendocino** (some b). **Merced:** 2 mi S Hilmar. **Modoc:** 5.5 mi E Cedarville (b). **Mono** (partly b). **Monterey. Napa:** 4 mi NW Berryessa, Samuel Springs. **Nevada:** Boca, Sagehen Creek near Hobart Mills (partly b). **Orange:** Irvine Lake. **Placer:** Carnelian Bay on Lake Tahoe (partly b), Foresthill, 4 mi S Rocklin. **Plumas:** Chilcoot (b), 4 mi W Quincy. **Riverside. Sacramento. San Benito:** Pinnacles National Monument. **San Bernardino:** Afton Canyon, Baldy Mesa, Big Bear Lake, Cajon Junction (also 4 mi W), Kramer Junction, Needles (also 20 mi N), Phelan, Twentynine Palms, Wildwood Canyon (5 mi E Calimesa), 3 mi SE Yucaipa. **San Diego. San Francisco** (b): San Francisco (Baker Beach, Laguna Puerca, Lake Merced, Lobos Creek, Lone Mtn., Marine Hospital, Presidio Park). **San Luis Obispo. San Mateo:** Redwood City, San Bruno Mts. (b). **Santa Barbara:** San Miguel Island (b), Santa Rosa Island. **Santa Cruz:** Felton, Lockhart Gulch (5 mi E Mt. Hermon). **Shasta:** 3 mi SW Old Station (partly b), Redding (b). **Sierra** (some b). **Siskiyou** (some b). **Sonoma** (some b). **Stanislaus:** Turlock. **Sutter:** Nicolaus. **Trinity:** Eagle Creek, Hayfork, Junction City. **Tuolumne:** Pinecrest, Poopanut Valley (Yosemite National Park), Tuolumne. **Ventura:** including San Nicolas Island (b). **Yolo:** Davis (partly b), Elkhorn Ferry, 5 mi SW Winters. **Yuba:** 18 mi NW Marysville, Smartville. COLORADO: **Weld:** Roggen (b). IDAHO: **Bear Lake:** Bear Lake. **Franklin:** 3 mi NW Preston. **Fremont:** St. Anthony (partly b), 6 mi NW St. Anthony (partly b). **Lincoln:** Dietrich Butte, Shoshone (also 18 mi E). **Owyhee:** 6.3 mi SE Murphy. KANSAS: **Clark:** —. **Douglas:** Lawrence. NEVADA: **Carson City:** Carson City (b). **Churchill:** Carson Sink, Fallon. **Clark:** Riverside. **Douglas:** Spooners Lake N junction Highway 28 (partly b). **Elko:** 25 mi S Elko (b). **Esmeralda:** 6 mi N 2 mi W Fish Lake. **Humboldt:** Orovada, Winnemucca (partly b). **Mineral:** Teels Marsh sand dunes. **Washoe** (some partly b). **White Pine:** —(b). NEW MEXICO: **Dona Ana:** 12 mi N Las Cruces, Mesilla Park. **Sierra:** Percha Dam State Park. OREGON: **Benton:** Corvallis (b), 10 mi S Corvallis (b). **Deschutes:** Smith Rock State Park. **Douglas:** Winchester Bay (b). **Jackson:** Laurelhurst State Park (b), Rogue River. **Lane:** Florence. **Lincoln:** Newport (b). **Umatilla:** Hermiston. **Wasco:** 7 mi E The Dalles (b). UTAH: **Cache:** Cornish (partly b), Logan (partly b). **Emery. Kane:** Kanab. **Millard:** 15 mi N Delta, 5 mi W Hatton, Kanosh (partly b). **Rich:** south shore of Bear Lake (b). WASH-

INGTON: **Jefferson:** Port Townsend (b). **Pacific:** Grassy Island (b), Nahcotta (b). WYOMING: **Carbon:** Rawlins (b). **Converse:** Glenrock (partly b). **Lincoln:** 18 mi S Jackson (b). **Sweetwater:** Rock Springs (partly b). **Teton:** Hoback Junction (b), Moran (partly b).

MEXICO: **Baja California Norte:** Cataviña (also 27 mi SE), 0.9 mi S El Cóndor, 4 mi S Santa María, Santa María Beach (San Quintín Bay).

Tachysphex antillarum Pulawski

(Figure 110)

Tachysphex antillarum Pulawski, 1974*a*:44, ♀, ♂. ! Holotype: ♀, Puerto Rico: Isla Verde (USNM).—Bohart and Menke 1976:272.

DIAGNOSIS.—*Tachysphex antillarum* has distinctive upper metapleural structures: an oblique carina beneath the fore end of the flange, and a prespiracular carina that extends from about midlength of the flange to the the metapleural hindmargin and is not angulate posteriorly. The male forefemur is entire, like *quisqueyus*, but unlike the other species of the *terminatus* group.

DESCRIPTION.—Frontal punctures well defined. Scutum punctures less than one diameter apart, but a few of them about one diameter apart. Metapleural flange broad; upper metapleuron with low, oblique carina beneath front end of flange, and with prespiracular carina that extends from about the midpoint of the flange to the metapleural hindmargin (carina not angulate posteriorly). Propodeum coarsely sculptured between dorsum and side. Basal tooth of hindcoxa large.

Vestiture obscuring integument from most angles between antennal socket and orbit.

Gastral segments I–IV black, remainder red. Terga I–IV silvery fasciate apically. Wings almost hyaline.

♀.—Clypeal width 3.2–3.4× length; bevel about as long as basomedian area; lip sinuate, slightly broadened mesally. Dorsal length of flagellomere I 1.7–1.9× apical width. Vertex width 1.8× length. Length 6.5–7.0 mm.

Length of setae about 1.3 MOD on vertex, 0.8 MOD on scutum anterolaterally.

♂.—Clypeal width 3.7× length. Dorsal length of flagellomere I 1.0–1.2× apical width. Vertex width 2.25× length. Sterna II–IV with glabrous, apical depression. Forefemur not emarginate. Foretarsus with rake; outer apical spine of foretarsomere II slightly longer than tarsomere III. Length 5.0–5.5 mm.

Setae length about 1.3 MOD on vertex, about 1.0 MOD on scutum anterolaterally.

GEOGRAPHIC DISTRIBUTION (Fig. 110).—Cuba, Puerto Rico.

MATERIAL EXAMINED.—3♀, 1♂, paratypes (CAS).

RECORDS (Pulawski 1974*a*).—CUBA: **Habana:** Jibacoa. **Las Villas:** Ciénega de Zapata. **Pinar del Río:** Guane, Pinales del Viñares.

PUERTO RICO: Isla Verde (airport)

Tachysphex ruficaudis (Taschenberg)

(Figures 109, 110)

Tachytes ruficaudis Taschenberg, 1870:12, ♀. ! Lectotype: ♀, Brazil: Nova Friburgo (Zool. Inst. Halle, Germany), designated by R. Bohart *in* Pulawski 1974*a*:37.—In *Tachysphex*: Jörgenson 1912:291; Pulawski 1974*a*:37 (full bibliography); Bohart and Menke 1976:276.

Tachytes pullulus Strand, 1910:169, "♀" = ♂. ! Lectotype: ♂, Paraguay: Villa Mora or Asunción (Zool. Mus. Berlin), designated by R. Bohart *in* Pulawski 1974*a*: 37. Synonymized by R. Bohart *in* Pulawski 1974*a*:37.

DIAGNOSIS.—*Tachysphex ruficaudis* can be recognized by the continuous carina (or, in some specimens, a few longitudinal ridges) starting beneath the anterior end of the metapleural flange

FIGURE 108. Geographic distribution of *Tachysphex clarconis* Viereck

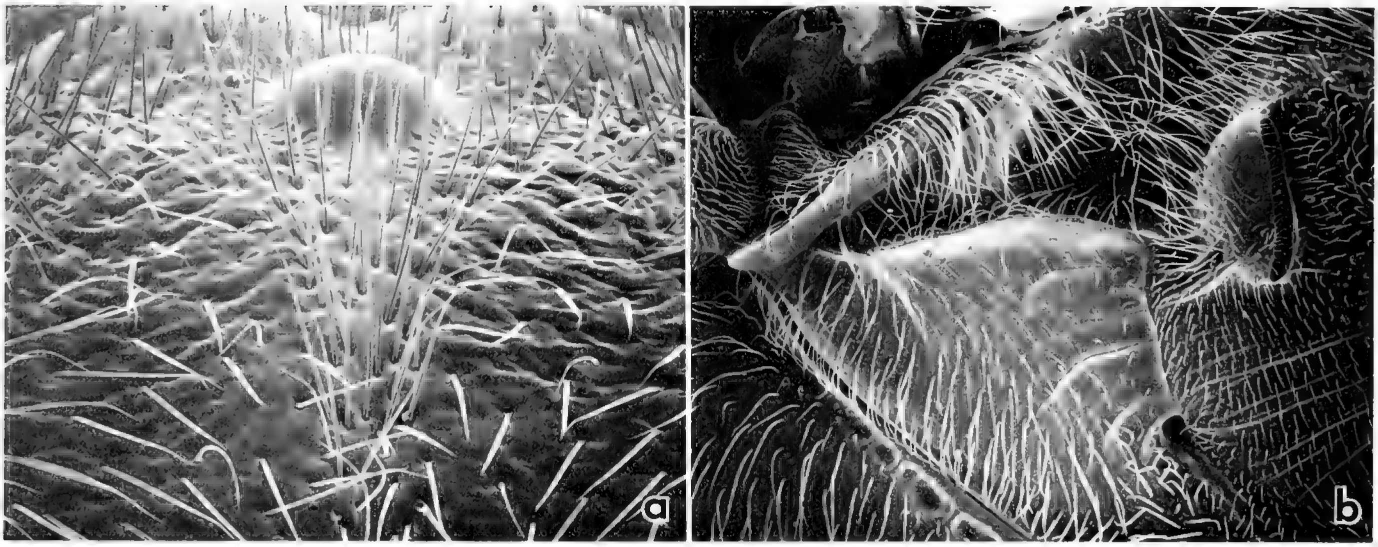

FIGURE 109. *Tachysphex ruficaudis* (Taschenberg), female: a—frons adjacent to midocellus; b—upper metapleuron, lateral view.

and ending before the propodeal spiracle (Fig. 109b). The broad metapleural flange distinguishes it from *clarconis*, *galapagensis*, and *peruanus*. Unlike other species of the *terminatus* group (except Bahamian *similis*), the mesopleural punctures of most *ruficaudis* are several diameters apart. The absence of a foretarsal rake distinguishes males of *ruficaudis* from other species of the group except *galapagensis*, *peruanus*, most *apicalis*, and some *linsleyi*.

DESCRIPTION.—Scutal punctures less than one diameter apart adjacent to margins and around admedian lines, and one to three to several diameters apart in remaining U-shaped area. Metapleural flange broad; upper metapleuron with one longitudinal carina (with a few longitudinal ridges in some individuals) that starts beneath anterior end of flange and ends before propodeal spiracle (Fig. 109b); carina obtusely angulate posteriorly in some Argentinian females; oblique carina beneath fore end of flange becoming higher toward flange, but abruptly lowering at attachment. Propodeum coarsely sculptured between dorsum and side in nearly all females and most males. Basal tooth of hindcoxa well developed.

Vestiture not obscuring or only partly obscuring sculpture between antennal socket and orbit.

Gastral terga I–IV (I–VI in some males) silvery fasciate apically. Wings moderately infumate.

♀.—Clypeal width 3.0–3.4 × length; lip evenly arcuate, mesally with small, obtuse projection in nearly all specimens. Dorsal length of flagellomere I 2.1–2.5 × apical width. Frons microrugose or closely punctate, with finely rugose interspaces (Fig. 109a). Vertex width 2.0–2.6 × length. Mesopleural punctures fine, several diameters apart (but large, less than one diameter apart in some Bolivian and Argentinian populations). Length 6–9 mm.

Setae length about 1.7–2.3 MOD on vertex, about 2.0 MOD anterolaterally on scutum.

Gaster with two or three apical segments red, all black in many specimens from Bolivia and south of the Tropic of Capricorn.

♂.—Clypeal width 3.2–3.6 × length; lip regularly arcuate, lateral corners sometimes slightly prominent, closer to antennal socket than to each other (sometimes equidistant). Frontal interspaces dull or shiny (occasional specimens), smooth or finely rugose. Vertex width 2.6–3.3 × length. Mesopleural punctures less than to much more than one diameter apart. Sterna III–VI glabrous or sparsely pruinose. Foretarsus mainly without rake, but some specimens with one or two preapical spines on forebasitarsus (spines shorter than basitarsal width); outer apical spine of foretarsomere II equal to corresponding inner spine or slightly longer. Length 5.0–6.5 mm.

Setae length about 2.0–2.5 MOD on vertex, about 1.7 MOD anterolaterally on scutum.

Gaster usually black, two apical segments reddish in some specimens.

GEOGRAPHIC DISTRIBUTION (Fig. 110).—Primarily a Neotropical species that invades the United States in Arizona and southern California. In the Caribbean Islands it only occurs in Jamaica. In South America it extends southward to 40°S.

MATERIAL EXAMINED.—60♀, 31♂ from North and Central America (CAS, CIS, CNC, FSCA, HKT, KU, LACM, MCZ, NYSU, SDNH, TAM, UAE, UAT, UCD, UCR, UIM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Coconino:** Oak Creek Canyon (1♀, TAM, 1♂, UAT). **Graham:** Bonita Creek (1♂, UAT). **Pima:** Molino Basin in Santa Catalina Mts. (1♀, UAT), Sabino Canyon in Santa Catalina Mts. (2♀, UCD), Tucson (1♂, CAS; 4♀, 2♂, UAT; 1♀, UI). **Pinal:** 3 mi W Superior (6♀, 3♂, CAS; 1♀, UAT). CALIFORNIA: **Riverside:** Andreas Canyon (1♀, UCD), Riverside (2♀, ♂, UCR). **San Diego:** La Mesa (1♀, SDNH), San Diego River (1♂, SDNH).

MEXICO: **Chiapas:** Montebello National Park, Suchiapa. **Jalisco:** Chamela, Estanzuela (40 km W Ameca), 15 mi NE Guadalajara, Puerto Vallarta, Tecolotlán. **Morelos:** 7.5 mi S Yautepec. **Nayarit:** Huajicori on River Acaponeta, San Blas. **Nuevo Leon:** 7 mi W El Cercado. **Quintana Roo:** Felipe Carillo Puerto (19°35′N, 88°03′W), Vallarta (17 km N Puerto Morelos). **Oaxaca:** Palomares. **San Luis Potosí:** El Naranjo El Salto, Tamazunchale. **Sinaloa:** Chupaderos, 54 mi S Culiacán, 8 mi SE Elota, Tabala, 20 mi E Villa Unión. **Sonora:** Alamos, Cócorit, E Yaqui River (35 air km WSW Sahuaripa). **Tamaulipas:** 15 mi N Llera. **Veracruz:** 30 mi S Acayucan, Atoyac, Cordoba, Coscomatepec, Fortín de las Flores, Orizaba, Puente Nacional. **Yucatan:** Uxmal.

CENTRAL AMERICA: BELIZE: Belize. COSTA RICA: 9 mi NW Esparta, Turrialba. EL SALVADOR: Parque Nacional del Cerro Verde, Quezaltepeque. PANAMA: Chiriquí (Potrerillos), La Chorrera, Portobelo, Taboga Island (Panama Province). **Canal Zone:** Barro Colorado, Cerro Cobre, Culebra–Arijan Trail, Empire.

JAMAICA: **St. Thomas Parish:** Yallahs (1♀, CAS).

FIGURE 110. Geographic distribution of *Tachysphex antillarum* Pulawski and *ruficaudis* (Taschenberg)

SOUTH AMERICA (localities listed in Pulawski 1974*a* are not repeated here) ARGENTINA: **La Pampa:** Sierra Lihuel Calel. COLOMBIA: **Cundinamarca:** 11 mi E Caqueza, Tolima Armero. PARAGUAY: San Pedro Caroro–Rio Ypane. PERU: **Huánuco:** Huánuco. TRINIDAD AND TOBAGO. **Trinidad:** Simla Field (Arima Valley). VENEZUELA: **Aragua:** Ocumar de la Costa. **Barinas:** 32 km E El Canton. **Falcón:** Peninsula Paraguana (Pueblo Nuevo). **Merida:** 15 km W Lagunillas. **Trujillo:** Sabana Grande. **Zulia:** Carrasquero, 32 km SW Machiques, Rio Palmar 15 km NE Rosario, Rosario. **Curaçao:** Willemstad

Tachysphex alpestris Rohwer

(Figures 111, 115)

Tachysphex foxii var. *alpestris* Rohwer, 1908:223, ♀, ! Holotype: ♀: Colorado: Teller Co.: Florissant (USNM).—As *Tachysphex alpestris* G. Bohart 1951:950, Bohart and Menke 1976:272, Krombein 1979:1630, Elliott and Kurczewski 1985:294, Rust et al. 1985:46.

Tachysphex terminatus: Evans 1970:491, corrected to *Tachysphex alpestris* by Kurczewski and Evans 1986:270, Elliott and Kurczewski 1970:103 (part).

DIAGNOSIS.—*Tachysphex alpestris* has a distinctive prespiracular prominence on the upper metapleuron: the prominence is low, obtusely angulate in side view, with the posterolateral margin markedly shorter than the anterior margin (Fig. 111b–d). Some *linsleyi* have a similar metapleuron and may be difficult to distinguish from *alpestris*, although either the prominence or the oblique carina is higher than in *alpestris* (most *linsleyi* have a distinctive prespiracular prominence; see that species for de-

tails). Wing color is also diagnostic: wings are hyaline in *linsleyi* and infumate to hyaline in *alpestris*. In *clarconis*, the metapleural flange is narrower than in *alpestris*, and the prominence is absent.

The metapleuron is similar in *alpestris* and the Caribbean species *antillarum*, but in the latter there is a short, nonangulate carina instead of a prominence; the clypeal lip of the female has a short, median projection; and the male forefemur is entire.

Description.—Frons punctate (Fig. 111a), but punctures ill defined in some specimens. Scutal punctures less than one diameter apart adjacent to margins and around admedian lines, but two or three to several diameters apart in remaining U-shaped area. Upper metapleuron, in front of propodeal spiracle, with low prominence that is obtusely angulate in side view (Fig. 111b, d), prominence consisting of a long anterior carina and two short posterior carinae (one carina in some specimens) that have a common apex (Fig. 111c); flange broad, oblique carina beneath its anterior end low, in most specimens becoming higher toward flange but lowering at attachment, absent in some specimens. Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa large or (some specimens) low, obtuse.

Vestiture not obscuring integument between antennal socket and orbit (except some populations from Nevada and California).

Terga I–IV or I–V silvery fasciate apically. Wings moderately infumate, hyaline in some specimens.

♀.—Clypeal width 2.6–3.0× length; bevel shorter than basomedian area; lip arcuate, without median projection. Dorsal length of flagellomere I 1.5–1.8× apical width. Vertex width 1.8–2.2× length. Length 6–9 mm.

Setal length about 2.0 MOD on vertex and about 1.3 MOD on scutum anterolaterally.

Gaster black (British Columbia), with two or three apical segments red (most United States populations) or all red (Desert Center and Borrego Valley, California; Mexico; Costa Rica).

♂.—Clypeal width 2.6–3.1× length; lip arcuate to straight; corners obtuse to acute, closer to antennal socket than to each other or slightly closer to each other. Vertex width 1.9–2.6× length. Sterna pubescent throughout or sterna II–VI glabrous apically. Foretarsus with rake; outer apical spine of foretarsomere II longer than tarsomere III. Length 4.5–7.0 mm.

Setal length about 1.7 MOD on vertex and 1.0–1.5 MOD on scutum anterolaterally.

Gaster black, rarely with red apical segment, all red in most Mexican and Costa Rican specimens.

Discussion.—*Tachysphex alpestris* may be a geographic form of *terminatus*. Both species are similar and differ mainly in the shape of the prespiracular prominence of the upper metapleuron. In Canada and the United States they are nearly allopatric (*alpestris* is western, *terminatus* is eastern), but they overlap in Alberta, Colorado, New Mexico, and Arizona. In Mexico and Central America, *alpestris* seems to be restricted to coastal habitats, while *terminatus* is also found inland. The species do not intergrade morphologically. The only possible intermediate was found in Playa Matanchen, Mexico. Of the five males from that locality (MCZ), three have a sharp prespiracular prominence (as in *terminatus*), one has an obtuse prominence (as in *alpestris*), and one an intermediate prominence. Otherwise these individuals are very similar to each other and look like representatives of a single population.

Life History.—The specimens from Jackson Hole, Wyoming, observed by Evans (1970) actually are *alpestris*, not *terminatus* as stated by the author (Kurczewski and Evans 1986). Prey transport was by flying. Two nests examined had one and three cells, respectively. The cells were placed 3.0–4.5 cm below the soil surface. The burrow was temporarily closed during the wasp's absence. Two to 13 immature grasshoppers were used per cell, all *Chorthippus curtipennis* (Harris), 5–9 mm long (mean 6.5 mm). Elliott and Kurczewski (1985) report a nymphal acridid, *Oedaleonotus* sp., as prey.

Three females examined were pinned with acridid prey: (1) one without locality label (CAS), determined as *terminatus* by F. E. Kurczewski, with two young nymphs of *Melanoplus* sp., 7.0 and 8.5 mm long, det. A. B. Gurney; (2) one from Sierra Valley, California (UCD), with four young nymphs of *Melanoplus*, probably *sanguinipes* (Fabricius), det. D. C. F. Rentz; and (3) one from the Arcata area, California (CAS), with a nymph, probably of *Microtes helferi* (Strohecker), det. D. Otte.

Geographic Distribution (Fig. 115).—Rocky Mountains to the Pacific Coast, also Manitoba; north to Alaska, south to Costa Rica. In the United States and Canada it replaces *terminatus* in the West.

Material Examined.—794♂, 850♀.

Records.—CANADA: **Alberta:** Drumheller, Edmonton, Lethbridge, Medicine Hat, 12 km SW Orion, Slave Lake, Writing-on-Stone Provincial Park. **British Columbia:** Comox, Lillooet, McGillivray Creek (Game Reserve near Chilliwack), Oliver, Penticton, Seton Lake, Vancouver, Vernon. **Manitoba:** Cormorant Lake. **Northwest Territories:** Rae, Yellowknife. **Saskatchewan:** Elbow, Prince Albert, Saskatoon

UNITED STATES: ALASKA: Alaska Highway mi 1246: 63°N, 142°W (22♂, NYSU, listed as *terminatus* by Elliott and Kurczewski 1978). ARIZONA: **Cochise:** Skelton Canyon (Peloncillo Mts.). **Coconino:** Flagstaff, 10 mi W Jacob Lake. CALIFORNIA: **Alameda. Alpine. Contra Costa. Del Norte:** Crescent City, Point St. George. **El Dorado:** Echo Lake, Grass Lake, Icehouse Road (24 air mi ENE Placerville) **Fresno. Humboldt. Inyo. Kern:** Short Canyon (7 mi NW Inyokern). **Lassen. Los Angeles. Marin. Mendocino. Modoc. Mono. Monterey. Nevada:** Boca, Olympia Lake, Sagehen Creek near Hobart Mills. **Orange:** Newport Beach, Santa Ana River. **Placer:** Carnelian Bay (Lake Tahoe), Forest Hill. **Plumas:** Blairsden, Greagle, Quincy. **Riverside. Sacramento:** Folsom, Sacramento. **San Bernardino:** 1–2 mi S Cajon Pass, Green Canyon (SE Sugarloaf), Phelan, Southern Fork of Santa Ana River, Thurman Flats Picnic Area, Victorville. **San Diego. San Francisco:** San Francisco (Baker Beach, Fort Funston, Laguna Puerca, Lake Merced, Lobos Creek, Presidio Park). **San Joaquin:** Corral Hollow (8 mi N Tracy). **San Luis Obispo. San Mateo. Santa Barbara:** including Santa Cruz Island. **Santa Clara:** Alum Rock, San Jose, Stanford University. **Shasta:** 2 mi W Shingletown. **Sierra. Siskiyou. Sonoma:** Bodega Bay, Mesa Grande. **Stanislaus:** Del Puerto Canyon, Turlock. **Trinity:** Coffee Creek Ranger Station, Hayfork Ranger Station, Mirror Lake **Tulare. Tuolumne. Ventura:** including Santa Barbara Island. **Yolo:** Davis, Elkhorn Ferry, 2 mi E Woodland. **Yuba:** Challenge. COLORADO: **Alamosa:** Great Sand Dunes. **Boulder:** Boulder. **Chaffee:** 1.5 mi N Salida. **Douglas:** 20 mi S Denver. **Eagle:** State Bridge near Bond Estes Park. **Garfield:** Rifle. **Gunnison:** 18–24 mi E Paonia. **Larimer. Mesa:** W end of Grand Mesa. **Moffat:** Greystone. **Montezuma:** 3 mi W Arriola. **Park:** Wilkerson Pass. **Routt:** 7 mi E Hayden. **Teller:** Florissant. **Weld:** Owl Creek 11 and 19 mi NE Nunn. IDAHO: **Bannock:** Pocatello. **Bear Lake:** Bear Lake, Paris. **Blaine:** 9 mi SW Bellevue, 3 mi NE Carey. **Bonner:** Walsh Lake Samuels. **Boundary:** Highway 95 (3 mi S British Columbia). **Butte:** Craters of the Moon National Monument. **Canyon:** Melba, Murphy, Notus, Parma. **Cassia:** Emery Canyon (12 mi SE Oakley), Sublette. **Custer:** Morgan Creek (5 mi NW Salmon River), Salmon River (2 mi N Challis), 5 mi NE Stanley. **Elmore:** Mayfield. **Franklin:** 3 mi NW Preston. **Fremont:** St. Anthony Sand Dunes. **Gooding:** 1 mi NE Gooding. **Idaho:** Lowell. **Jefferson:** 6 mi N Roberts. **Jerome:** Hunt Project (2 mi N Hazelton). **Kootenai:** Lane. **Latah:** 5 mi N Bovill, Idlers Rest near Moscow **Nez Perce:** Lewiston. **Oneida:** Black Pine Canyon, Holbrook Sand Dunes. **Owyhee:** 17 mi W Silver City, Walter's Ferry. **Twin Falls:** Rogerson, Twin Falls. **Valley:** Darling's Flat (S Fork Salmon River), Donnelly. MONTANA: **Toole:** 27 mi E Shelby. NEBRASKA: **Madison:** Meadow Grove. NEVADA: **Churchill:** 1 mi W Eastgate, Fallon, 3 mi W Hazen. **Douglas:** Kingsbury Summit, Spooners Lake (N

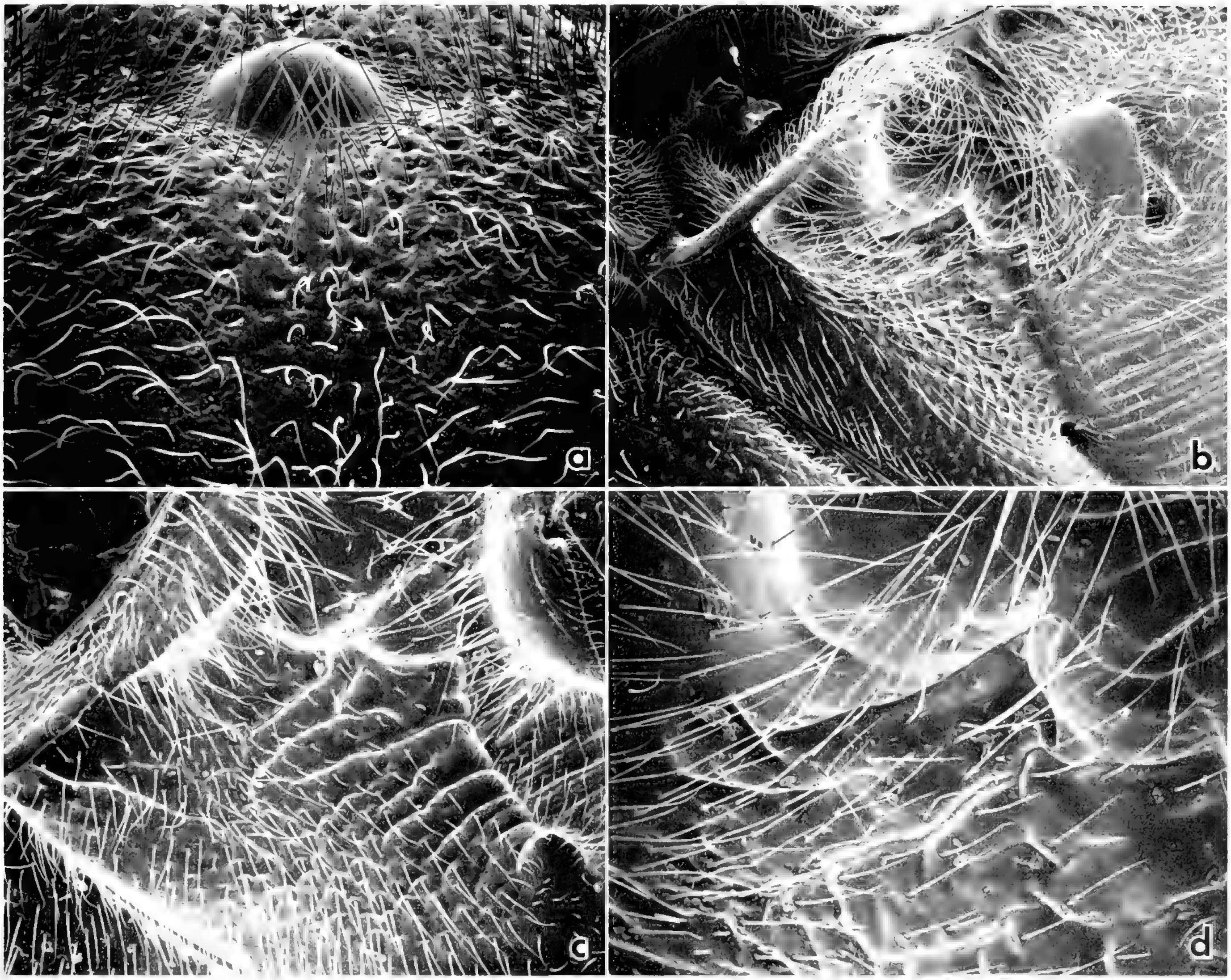

FIGURE 111. *Tachysphex alpestris* Rohwer, female: a—frons adjacent to midocellus; b—upper metapleuron, lateral view, c—same, top view; d—prespiracular prominence of upper metapleuron.

Junction Highway 28), Topaz Lake. **Elko. Eureka:** Boewowawe, Diamond Valley **Humboldt:** Canyon Creek, Orovada. **Lander:** Austin. **Lincoln:** Panaca. **Nye:** 5 mi N Round Mt. **Pershing:** 7 mi E Oreana **Storey:** Geiger Gd. **Washoe. White Pine.** NEW MEXICO: **Catron:** Pie Town. **Colfax:** Raton, 2 mi N Ute Park. **Sandoval:** Jemez Springs. **Taos:** Taos. OREGON: **Baker:** Cornucopia **Coos:** —. **Crook:** Powell Butte. **Curry:** Gold Beach **Deschutes:** Deschutes River 1 mi SW Pringle Falls, 9 mi E Redmond, Tumalo Res **Douglas:** Winchester Bay. **Jackson:** Rogue River (Palmerton Arboretum) **Lake:** Drake Peak **Lane:** Florence. **Lincoln:** Newport **Linn:** Lost Lake. **Tillamook:** Rockway. **Union:** Union. UTAH. **Box Elder:** Fielding **Cache. Duchesne:** 5.5 mi W Roosevelt. **Emery:** Huntington Creek, Wild Horse Creek W Goblin Valley. **Garfield:** Calf Creek, SSE Notom (Blind Trail Wash, Sweetwater Creek), Shootaring Canyon. **Juab:** Mt. Nebo. **Millard:** Delta, 5 mi W Hatton. **Rich:** Garden City, Logan Canyon summit. **Salt Lake:** Salt Lake City. **San Juan:** Blanding, Kane Springs (E Bridges National Monument). **Summit:** Coalville. **Uintah:** 17 mi S Bonanza, 6 mi N Vernal. **Utah:** Salem, Spanish Fork. **Washington:** Duncan Flats, Upper Deep Creek, Zion National Park. **Wayne:** Hanksville. **Weber:** Willard Basin. WASHINGTON. **King:** Richmond Beach, Seattle. **San Juan:** Argyle. **Thurston:** Olympia. **Walla Walla:** Mill Creek, Walla Walla **Whitman:** Wawawai County Park. **Yakima:** Yakima River. WYOMING. **Fremont:** Kinnear. **Laramie:** 28 mi E Laramie. **Natrona:** Powder River. **Park:** Sunlight Basin N Cody. **Sublette:** 3 mi N Pinedale. **Sweetwater:** Farson (also 20 mi E), Granger, 12 mi S Green River. **Teton:** 6 mi N Jackson, Jackson Hole Biological Station (Moran), Pilgrim Creek, Snake River (5 mi S Elk)

MEXICO: **Baja California Norte:** 1 mi S El Condor, 15 mi E Ensenada, 6 mi N Laguna Hanson (Sierra Juarez) **Baja California Sur:** Todos Santos **Chiapas:** Puerto Madero **Jalisco:** Playa Cuitzamala 8 km S Careyes **Nayarit:** Playa Matanchen near San Blas **Sinaloa:** Mazatlan **Tamaulipas:** Municipio Aldama, Rancho Nuevo, Barra Coma (1♀, CAS, 2♀, 1♂, FSCA) **Yucatan:** Progreso

COSTA RICA Limon

Tachysphex linsleyi R. Bohart

(Figures 112, 113)

Tachysphex linsleyi R. Bohart, 1962:35, ♂, ♀. Holotype ♂, Nevada Churchill Co 1 mi W Eastgate (CAS).—Krombein 1967:393. Bohart and Menke 1976:274. Krombein 1979:1931

DIAGNOSIS.—Most *linsleyi* can easily be recognized by the shape of the upper metapleuron: the oblique carina beneath the anterior end of the flange is partly translucent and expands to the outer edge of the flange or nearly so; the prespiracular prominence of the upper metapleuron is funnel-shaped, partly translucent (Fig. 112a–c). Both structures vary in size and in some specimens they approach the condition found in *alpestris*

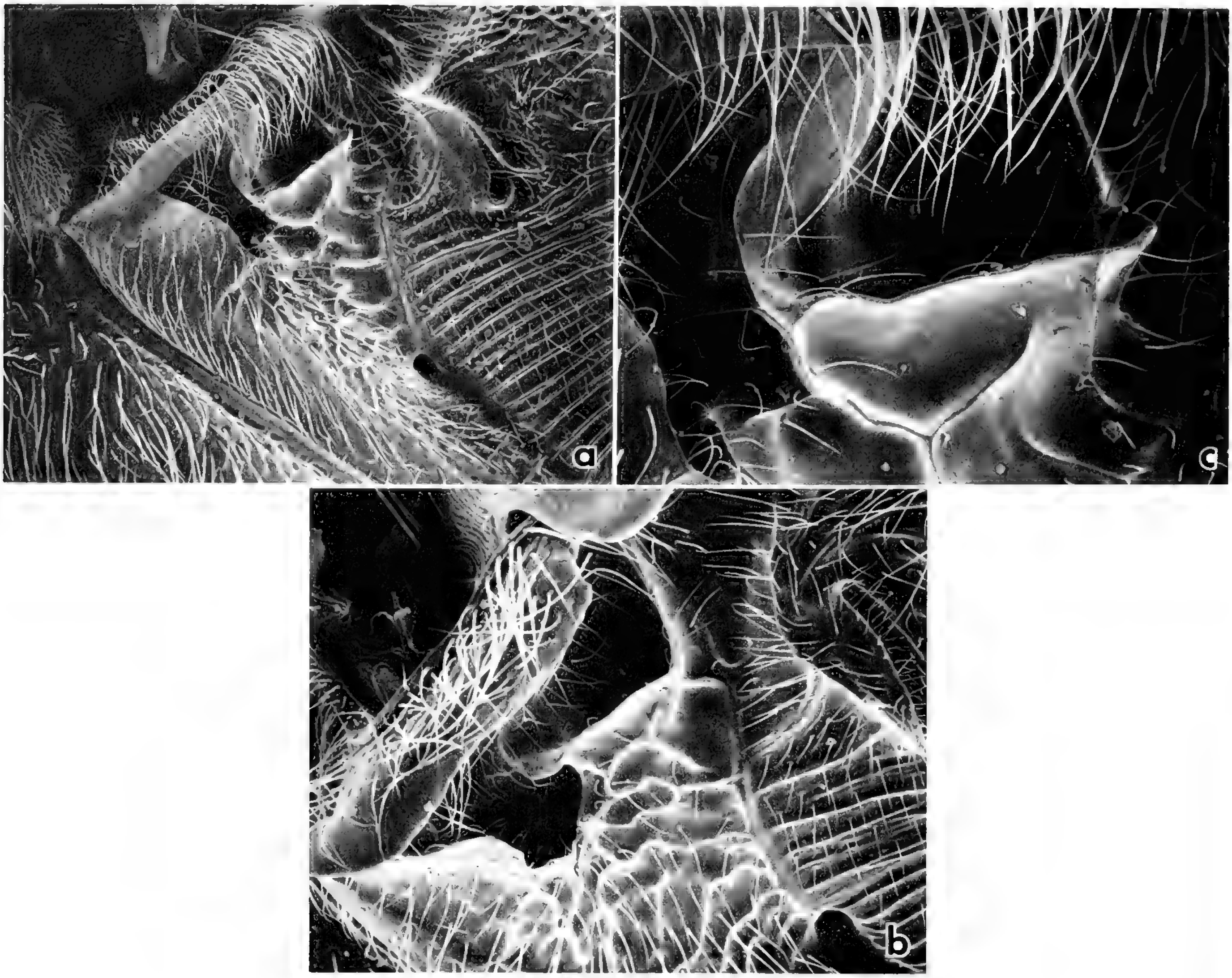

FIGURE 112. *Tachysphex linsleyi* R. Bohart, female: a—upper metapleuron, lateral view; b—same, top view; c—prespiracular prominence of upper metapleuron.

The hyaline wings of *linsleyi* help in recognition (wings hyaline to infumate in *alpestris*).

DESCRIPTION.—Frons with well-defined punctures. Scutal punctures less than one diameter apart adjacent to margins and around admedian lines, but about one to several diameters apart in remaining U-shaped area. Upper metapleuron with prespiracular prominence which consists of three carinae having a common apex (Fig. 112a–c): a long anterior carina, a long admedian carina, and a short posterior carina (the latter inconspicuous in some individuals); the anterior and admedian carinae in most specimens high and partly translucent, intersecting at an obtuse angle and forming a funnellike structure; these two carinae low, ridgelike in some specimens, only slightly higher than in *alpestris*; metapleural flange broad; oblique carina beneath its anterior end becoming higher toward flange, highest at the attachment; in many specimens it is largely translucent and as high as flange (its upper margin meeting outer margin of flange), but low, slightly higher than in *alpestris*, in some individuals. Mesopleural punctures well defined, less than one diameter apart (some punctures may be more than one diameter apart). Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa large.

Vestiture totally obscuring sculpture between antennal socket and orbit.

Terga I–IV (female) or I–V (male) silvery fasciate apically. Wings hyaline.

♀.—Clypeus width 2.8–3.0× length; lip arcuate, without median projection. Dorsal length of flagellomere I 1.5–2.2× apical width. Vertex width 2.0–2.4× length. Length 7–9 mm.

Setal length almost 2.0 MOD on vertex, about 1.7 MOD anterolaterally on scutum.

Gaster black, usually with three apical segments red, all black in two Arizona females: from Bouse (ASU) and Tucson (UAT); largely or all red in some California specimens; only segment I and part of II black in one of the females from Antelope Springs (CIS), in a single female seen from Desert Center (NYSU), and

one from Anza (UCD); gaster all red in two females from Death Valley Junction (UCD), and a female from Tucson, Arizona (UAT).

♂.—Clypeal width 2.6–2.9 × length; lip arcuate; corners distinct but not prominent, closer to each other than to antennal socket or equidistant. Vertex width 2.3–2.8 × length. Terga II–VI glabrous apicomesally. Foretarsal rake present in most specimens, but absent in two males from Sierra de la Giganta, Baja California Sur (CAS); outer apical spine of foretarsomere II longer than foretarsomere III. Length 4.5–7.0 mm.

Setal length about 2.0 MOD on vertex, about 2.5 MOD anterolaterally on scutum.

Gaster black, three or four apical segments red; only segment I black in many specimens from Death Valley Junction, California.

Life History.—Krombein (1967) recorded unidentified acridid nymphs as prey of *linsleyi*. A female from Rodeo, New Mexico (UCD) is pinned with her prey, an immature acridid *Eremiacris pallida* (Bruner), determined by D. C. F. Rentz.

Geographic Distribution (Fig. 113).—Western United States and Mexico, north to Washington and Idaho, south to central Mexico, east to Colorado and Texas.

Material Examined.—290♀, 309♂ (on the 19♀, 4♂ paratypes from Eastgate, Nevada, 1♀ is actually *apicalis*, and 5♀, 1♂ are *alpestris*).

Records.—UNITED STATES: ARIZONA: **Apache:** Eagar, Vernon. **Cochise. Coconino:** 15 mi N The Gap. **Gila:** Gila River 3 mi S Christmas. **Graham:** Roper Lake State Park (6 mi S Safford). **Maricopa. Mohave. Pima:** Santa Rita Mts., Tucson. **Pinal:** Maricopa, Superior (Boyce Thompson Arboretum). **Yavapai:** 7 mi E Cottonwood. **Yuma:** 5 mi SE Bouse, Parker. CALIFORNIA: **Fresno:** 3 mi N Pine Ridge. **Imperial:** Chocolate Mts. (Ogilby Road 3 mi S Junction Highway 78), Glamis. **Inyo. Lassen:** Hallelujah Junction. **Los Angeles:** 12 mi NE Pearblossom. **Mono:** Paradise Camp. **Riverside. Sacramento:** Sacramento. **San Bernardino. San Diego:** Borrego Valley, 10 mi NE Ramona. COLORADO: **Baca:** Two Buttes Reservoir. **Bent:** Hasty. **Garfield:** Rifle. **Larimer:** Fort Collins, Park Creek (20 km N Fort Collins). **Pueblo:** Pueblo. **Weld:** Owl Creek (11 mi NE Nunn). IDAHO: **Ada:** 12 mi NW Regina. **Canyon:** Marsing, 2 mi W Melba. **Cassia:** Murtaugh. **Elmore:** Hammett. **Franklin:** Preston. **Gooding:** Wood River 1 mi NE Gooding. **Oneida:** 5 mi NW Holbrook, Salyer Cow Camp, Stone Reservoir. **Owyhee:** 4 mi SW Bruneau. MONTANA: —. NEVADA: **Churchill:** 1 mi W Eastgate. **Clark:** 20 mi W Glendale, Grand Gulch Road 22 air mi S Mesquite. **Humboldt:** Orovada. **Lincoln:** Panaca. **Mineral:** —. **Nye:** 24 mi E Tonopah. **Washoe:** Patrick. NEW MEXICO: **Bernalillo:** Albuquerque. **Catron:** Pie Town. **De Baca:** Sumner Lake State Park. **Dona Ana:** Hatch, Las Cruces (also 15 mi N). **Eddy:** 5 mi N Carlsbad. **Hidalgo. Luna:** Cooks Mts. **McKinley:** Tohatchi. **Otero:** Alamogordo. **San Juan:** 43 mi S Shiprock. **Sierra:** Percha Dam State Park. **Socorro:** La Joya (20 km N Socorro). **Torrance:** Gran Quivira (town). OKLAHOMA: **Cimarron:** Black Mesa State Park. OREGON: **Deschutes:** 9 mi E Redmond. TEXAS: **Brewster:** Big Bend National Park, 1 mi W Lajitas. **Cameron:** Brownsville, Port Isabel. **Hudspeth:** McNary, 5 mi E Sierra Blanca. **Presidio:** 3 mi E Presidio. **Uvalde:** Nueces River. **Victoria:** Victoria. **Ward:** 1 mi S Grandfalls. UTAH: **Box Elder:** Promontory, 15 mi W Tremonton. **Cache:** Cornish. **Emery:** N Goblin Valley (Wild Horse Creek), 15 mi NW Woodside. **Garfield:** Blind Trail Creek SSE Notom, Calf Creek, Shootaring Canyon. **Grand:** Salt Valley NW Arches National Park. **Millard:** 12 mi W Fillmore. **San Juan:** 25 mi S Moab. **Tooele:** St. John. **Uintah:** SW Bonanza, Green River 5 mi NE Jensen. **Utah:** Goshen. **Washington:** Leeds Canyon, Paradise Canyon, Zion National Park. WASHINGTON: **Asotin:** Clarkston. WYOMING: **Natrona:** Powder River

MEXICO: **Baja California Norte:** Cataviña, 7.6 mi San Vicente. **Baja California Sur:** 12 mi S Guillermo Prieto, 13 air km WNW La Purisima, 16 mi E Rosarito, 3.5 km WNW San Isidro, Sierra de la Giganta (22 km W Loreto), E edge of Sierra Placeres (27°35′N, 114°30′W), 11 mi NE Todos Santos. **Chihuahua:** 20 mi N Ciudad Camargo, Colonia Juárez, 9 mi S Hidalgo del Parral. **Coahuila:** San Pedro de las Colonias (also 25 mi SE). **Sinaloa:** 54 mi S Culiacán, 8 mi SE Elota. **Sonora:** 10 mi SE Alamos, 6 km NNW San Carlos. **Tamaulipas:** Matamoros (also 30 mi SE). **Zacatecas:** 9 mi N Ojocaliente.

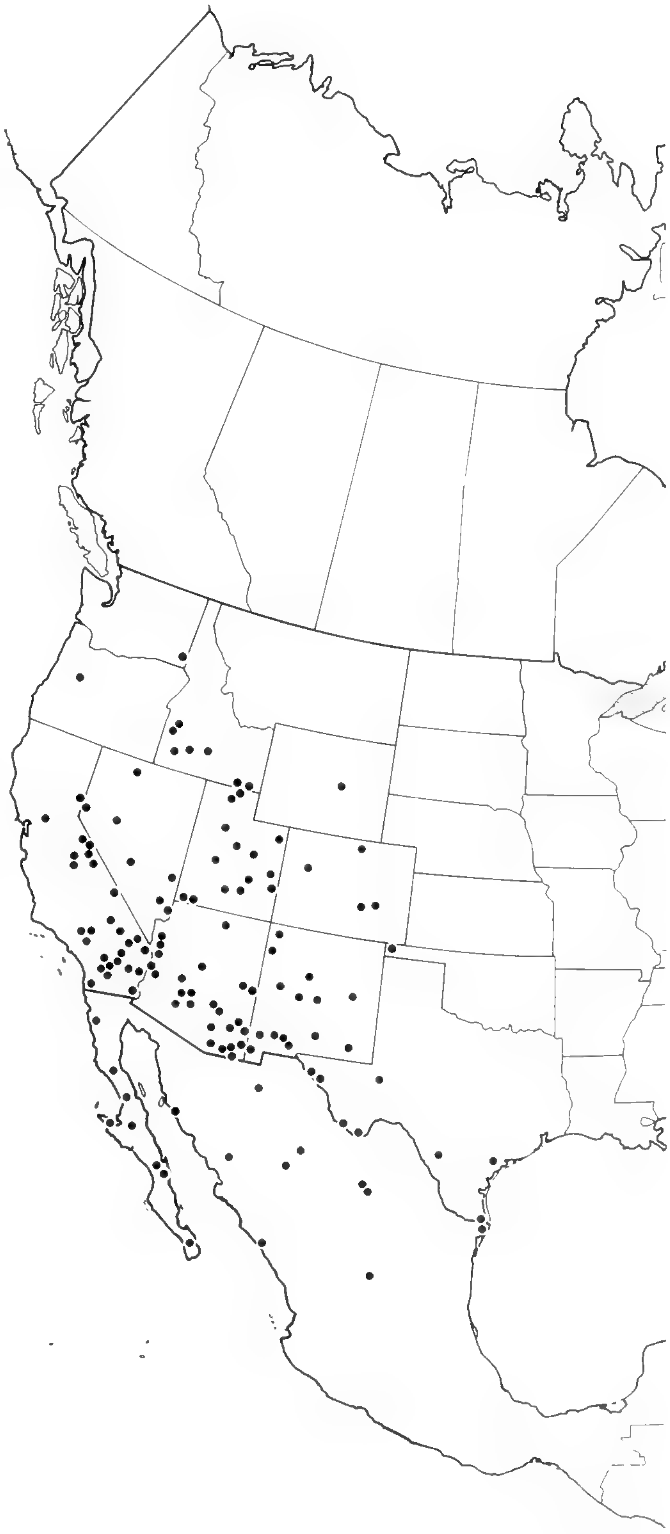

Figure 113. Geographic distribution of *Tachysphex linsleyi* R. Bohart

Tachysphex quisqueyus sp. n.

(Figure 115)

Derivation of Name.—Quisqueyus is a neo-Latin adjective derived from Quisqueya, the oldest known name of Hispaniola (the island was so called by the Tano Indians, its original inhabitants); an allusion to the geographic distribution of this species.

Diagnosis.—*Tachysphex quisqueyus* is known only from Hispaniola and is the only member of the *terminatus* group found on that island. It shares with *antillarum* the nonemarginate male forefemur (emarginate basally in the other members of the *terminatus* group). It differs from *antillarum* in the structure of the upper metapleuron: the prespiracular prominence is high, toothlike, and the oblique carina beneath the fore end of the flange is high, conspicuous (prominence and oblique carina low, inconspicuous in *antillarum*). Three other species have metapleural structures similar to *quisqueyus*, but differ as follows (characters in parentheses refer to *quisqueyus*). In *apicalis*, the clypeus is narrow (clypeus broad, see Description below for the proportions) and the frons is shiny (frons dull); in *similis*, frontal punctures are indistinct, and the prespiracular prominence is sharp in most specimens (frontal punctures well defined, prespiracular prominence obtuse); in *terminatus*, the width of the female vertex is 2.0–2.2 × length, and the vestiture completely conceals the basal portion of the clypeus (vertex width in female 1.6–2.0 × length, clypeal vestiture not obscuring the integument). In addition, all or nearly all scutal punctures are less than one diameter apart in *quisqueyus* (scutum almost uniformly punctate), whereas in most specimens of the other three species the scutum is densely punctate along margins and behind admedian lines but sparsely punctate in the remaining U-shaped area.

Description.—Frontal punctures well defined. Scutal punctures in some specimens less than one diameter apart, or one or more diameters apart in a U-shaped area (a few largest interspaces up to two or three diameters). Upper metapleuron with large, toothlike prominence in front of propodeal spiracle (prominence similar to that of *terminatus*); flange broad; oblique carina beneath its anterior end becoming higher toward flange but abruptly lowering at its attachment. Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa large.

Vestiture obscuring integument from most angles between antennal socket and orbit, but not obscuring clypeal integument. Setae length about 1.7 MOD on vertex, 1.3 MOD on scutum anterolaterally.

Gastral segments I–IV black, remainder red. Terga I–IV silvery fasciate apically. Wings weakly infumate.

♀.—Clypeal width 2.9–3.2 × length; lip arcuate. Dorsal length of flagellomere I 1.7–1.9 × apical width. Vertex width 1.7–2.0 × length. Length 5.5–7.5 mm.

♂.—Clypeus width 3.1–3.6 × length. Dorsal length of flagellomere I 1.25 × apical width. Vertex width 1.9–2.1 × length. Sterna pubescent throughout. Forefemur entire. Foretarsus with rake; outer apical spine of foretarsomere II longer than foretarsomere III. Length 3.5–6.0 mm.

Geographic Distribution (Fig. 115).—Hispaniola.

Material Examined.—Holotype: ♂, Dominican Republic: Provincia Pedernales, Cabo Rojo, 5 Nov 1986, WJP (CAS, Type #15910).

Paratypes (13♂, 48♀). DOMINICAN REPUBLIC: **Distrito Nacional:** Haina, 18–24 May 1985, H. L. Dominguez (1♀, FSDA), 30 May 1985, LAS (2♀, FSCA), 1 and 8 Nov 1986, WJP (2♀, 7♂, CAS). **Monte Christi:** 9 km N Monte Christi, 17 June 1986, LAS and R. E. Woodruff (1♀, FSCA). **Pedernales:** Cabo Rojo, 4 and 5 Nov 1986, WJP (4♀, 38♂, CAS; 2♂, MCZ). **San Pedro de Macoris:** Boca del Soca, 13 June 1976, EEG (3♀, 1♂, FSCA).

Tachysphex terminatus (F. Smith)

(Figures 114, 115)

Larrada terminata F. Smith, 1856:291, ♂. ! Lectotype: ♂, labeled "Trenton Falls, New York" (Oxford Univ. Mus., England), present designation.—Cresson 1862: 238, 1872:214, 1876:208.—In *Larra*: Patton 1881:389; Provancher 1882:50, 1883:633, 1887:267 (in key); Kohl 1885:248; Ashmead 1899:250; Cockerell 1900:144; J. Smith 1900:518; Harrington 1902:221; H. Smith 1908:382; J. Smith 1910:683; Williams 1914:172, 201; Rohwer 1916:687, 1917*b*:244; Mickel 1918:422; Rau and Rau 1918:144; Washburn 1918:223; Rau 1926:188; Bradley 1928:1009; Robertson 1928:195, 209; Brimley 1938:443; Rau 1946:10; Krombein 1950:267; G. Bohart 1951:953; Krombein 1952:93; Cooper 1953: 33; Krombein 1953*a*:295, 296, 330, 1953*b*:123, 132; Strandtmann 1953:49; Evans 1958:118 (larva); Krombein 1958*b*:100, 1958*c*:188; Kurczewski and Kurczewski 1963:146; Kurczewski 1966*a*:317, 1966*b*:436–453; Krombein 1967: 393; Kurczewski 1967:279; Kurczewski and Harris 1968:81; Kurczewski and Snyder 1968:28; nec Evans, 1970:491 (=*Tachysphex alpestris*); Miller and Kurczewski 1973:210; Steiner 1973:24; Elliott and Kurczewski 1974:725; Pulawski 1974*a*:41; Elliott and Kurczewski 1975:268; Bohart and Menke 1976:277; Elliott and Kurczewski 1978:103; Krombein 1979:1631; Finnamore 1982:107; Spofford and Kurczewski 1984:663; Spofford et al. 1986:350.

Larra minor Provancher, 1887:268, ♀, ♂. ! Lectotype: ♂, Ontario: Ottawa (Laval Univ., Quebec), designated by Gahan and Rohwer 1917:433. Synonymized by W. Fox 1894*a*:520 and G. Bohart 1951:953 (as syn. n.).

Diagnosis.—A conspicuous feature of *terminatus* is the toothlike prespiracular prominence on the upper metapleuron, with the anterior and the posterior margin about equal in length (Fig. 114b–d). A similar structure is found in *apicalis*, *quisqueyus* (see these species for differences), and in *similis*. In *terminatus* the metapleural prominence is broad in lateral view (narrow in most *similis*, Fig. 116d) and, in addition, frontal punctures of most specimens are well defined (ill defined in *similis*). In the female of *terminatus* the vertex width : length ratio is 2.0–2.2 (1.4–1.7 in *similis*), the anterolateral scutal setae are about 2.0 MOD (about 1.0 MOD in *similis*), and the setae entirely conceal integument between antennal socket and orbit (partly so in *similis*). The males of the two species are difficult to distinguish. In *terminatus*, the frontal punctures are well defined in most specimens (frons microrugose, with punctures ill defined or absent, in most *similis*); the vertex averages wider (width : length ratio 2.0–2.5, and 1.6–2.2 in *similis*), the anterolateral scutal setae are somewhat longer (about 2.0 MOD instead of about 1.3), and the integument between the antennal socket and orbit is totally concealed by setae in most specimens (not concealed in *similis*).

Description.—Clypeal width 3.0–3.2 × length (2.8 × in small females). All scutal punctures less than one diameter apart in some specimens (e.g., in a female from Washington, D.C., CAS), but in most individuals punctures less than one diameter apart adjacent to margins and around admedian lines, and one or two to several diameters apart in remaining U-shaped area. Upper metapleuron (Fig. 114c–d): flange broad; oblique carina beneath its anterior end becoming higher toward flange but abruptly lowering at its attachment, lamelliform in many specimens; prominence before propodeal spiracle conspicuous, consisting of three carinae which have a common apex: anterior and posterior carinae (which are about equal in length), and admedian carina. Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa well developed.

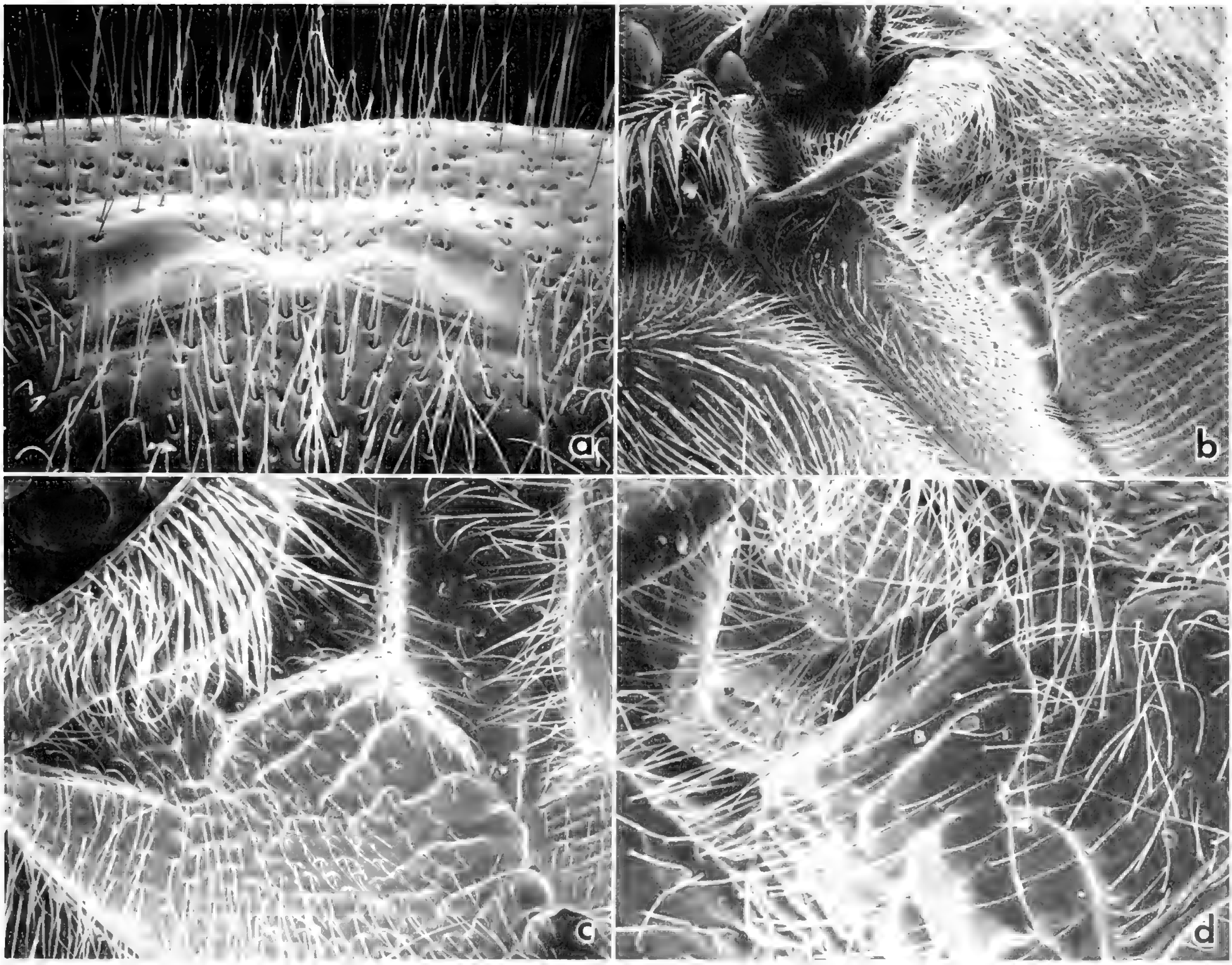

FIGURE 114. *Tachysphex terminatus* (F. Smith): a—hindocellar area of female; b—upper metapleuron, lateral view; c—same, top view; d—prespiracular prominence of upper metapleuron.

Vestiture totally obscuring sculpture between antennal socket and orbit (except in small males).

Gaster in most specimens with two or three apical segments red, but all black in several females from Ontario, and also in some females from New Jersey (Vineland, 1♀, CU; Westville, 1♀, ANSP) and New York (Broadalbin, 1♀, NYSU). Terga I–IV silvery fasciate apically. Wings hyaline to moderately infumate.

♀.—Clypeal lip arcuate, sometimes with obtuse, median projection. Dorsal length of flagellomere I 1.4–1.8 × apical width. Frons punctate to (some specimens) punctatorugose. Vertex width 2.0–2.2 × length. Length 6.5–10.0 mm.

Setal length about 2.0 MOD on vertex and anterolaterally on scutum.

♂.—Clypeal lip arcuate to almost straight, lateral corners sometimes prominent, usually closer to antennal socket than to each other (sometimes equidistant). Frons punctate, punctures subcontiguous. Vertex width 2.0–2.5 × length. Sterna III–IV glabrous, at least posteriorly. Foretarsal rake well developed; outer apical spine of foretarsomere II longer than tarsomere III. Length 5–8 mm.

Setal length about 1.7 MOD on vertex and about 2.0 MOD anterolaterally on scutum.

VARIATION.—The size of *terminatus* varies seasonally (Elliott and Kurczewski 1975): females of the first generation store more prey and a larger biomass, with the result that second generation females are slightly larger; the latter store less food, and consequently first generation females are slightly smaller. Elliott and Kurczewski (1974) also found size displacement in a mixed colony of *terminatus* and *similis* in Pottawatomie Co., Kansas. Individuals of *terminatus* averaged larger than in allopatric situations, individuals of *similis* averaged smaller.

The geographic variation of *terminatus* was analyzed by Elliott and Kurczewski (1978), but they actually confused two species: *alpestris* and *terminatus* (but see Remark under *alpestris*). I have seen the material.

LIFE HISTORY.—There are two generations per year in the northeastern United States (Elliott and Kurczewski 1974), emerging in June and August, whereas Strandtmann (1953) thinks that five generations per year are possible in Texas. The flight period in Texas is from May through October (Strandtmann

1953), but I examined a female from Bentsen Rio Grande Valley State Park, Texas (USNM) collected as late as 30 November–2 December). Krombein (1951) observed individuals feeding on tulip-tree honeydew produced by *Toumeyella liriodendri* (Gmel.), and also (1953*a*) on foliage of *Quercus marilandica* Muench., *Carya* sp., and *Pinus serotina* Michx. Robertson (1928) found *terminatus* on flowers of *Cicuta maculata* L. and *Sium suave* Walt. (=*cicutaefolium* Schrank). The species is gregarious: Kurczewski and Harris (1968) found 12 cells in each of two plots of about 0.5 m^2, Strandtmann (1953) found 10 cells in a square foot, and Kurczewski (1966*b*) noted about 50 males on a sandy area about 4.0 × 1.8 m.

Habits of *terminatus* have been extensively studied by Kurczewski (mainly in coauthorship, see citations above) and others. Females nest in flat or sloping sandy areas with sparse vegetation, and in harder soil or clay (Rau and Rau 1918; Rau 1926). Those digging in sand seldom abandon unfinished nests, but in clay they often dig several burrows in succession before completing a nest (Rau and Rau 1918). The nest may have one to five cells, usually two or three. It is a regular gallery when excavated in sand, but "in hard earth it has any shape and size that they can best excavate" (Rau and Rau 1918). The gallery is oblique to the soil surface. It is 6.2–10.8 cm long in sand, with its lower end 4.2–5.7 cm below the surface (3 cm according to Strandtmann 1953). However, nests dug in the loose dirt on the top of a clay bank (Rau 1926) were so shallow that they could be exposed by blowing. Normally, the nest entrance is temporarily closed during the provisioning period. However, the nest is sometimes established on steep slopes so that excavated sand rolls down and cannot be reused for temporary closure (Kurczewski and Snyder 1968). In such situations, the closure is incomplete. The nest may also remain open as the result of high temperatures: Miller and Kurczewski (1973) observed a female making only a token effort to close the nest before leaving, when the sand temperature was 62°C (at 49°C, the wasp simply entered the nest by digging away the sand; at 57°C she dug more rapidly, but four digging periods separated by three short hovering flights were necessary for the wasp to gain entry). Orientation flights are performed after completion of the nest (F. E. Kurczewski, pers. comm.). Prey consists of first- and second-instar Acrididae nymphs and rarely includes Tettigoniidae (see below for details). The mean length of 906 acridid prey from Groton, New York, is about 6.8 mm (Kurczewski 1966*a*; Evans 1970). Known acridid prey are listed below:

Prey	Source
Arphia sulphurea (Fabricius)	Rau 1946
Chloealtis conspersa (Harris)	Kurczewski 1966*a*
Chorthippus curtipennis (Harris)	Kurczewski 1966*a*
Chortophaga viridifasciata (DeGeer)	Ashmead 1894, Rau 1926
Dichromorpha viridis (Scudder)	Rau and Rau 1918; Rau 1946
Dissosteira carolina (Linnaeus)	Kurczewski 1966*a*
Melanoplus bivittatus (Say)	Kurczewski 1966*a*
Melanoplus femurrubrum (DeGeer)	Kurczewski 1966*a*
Melanoplus keeleri luridus (Dodge)	Kurczewski 1966*a*
Melanoplus sp.	Rau and Rau 1918, Rau 1946; Strandtmann 1953
Oedipodid nymphs	Rau and Rau 1953
Pardalophora apiculata (Harris)"	Kurczewski 1966*a*
Syrbula admirabilis (Uhler)	Rau and Rau 1918
Tryxaline nymph	Williams 1914

G. Bohart's (1951) record of Tetrigidae as prey of *terminatus* (repeated in Bohart and Menke 1976) is probably erroneous. I have been unable to confirm this. Strandtmann (1953) recorded *Tryxalus* sp., but the record cannot be accurate, because *Tryxalus* is not a New World genus (Finnamore 1982).

The grasshopper prey are flown to the nest, head forward and venter up. The prey's antennae are grasped by the mandibles of the wasp and her legs embrace the hopper's body. However, Strandtmann (1953, fig. 2) drew a nymph held venter down during transport. The prey is dropped on the ground venter up, while the wasp opens the nest. She then enters the burrow, turns around inside, emerges headfirst, and reenters backwards, pulling the prey inside by its antennae. One female provisioning the nest dug in a steep slope and incompletely closed, entered the nest without first dropping the grasshopper (Kurczewski and Snyder 1968).

The occasional use of tettigoniid instead of acridid prey at Groton, New York is especially interesting (Kurczewski 1966*a*). From 1960 to 1963 he examined 926 prey, all Acrididae. However, four small tettigoniid nymphs were collected by at least three wasps (possibly four) in June 1964. Kurczewski's prey were determined by A. B. Gurney as *Phaneroptera*, but as Finnamore (1982) points out, *Phaneroptera* is not a New World genus. At my request, David A. Nickle of the U.S. Department of Agriculture reexamined the specimens and found that they are a *Scudderia*, probably *furcata* Brunner von Wattenwyl. Only one acridid species, *Melanoplus bivittatus* (Say), was stored in the cell with *Scudderia*. A scarcity of grasshopper nymphs of suitable size may have been the reason for the wasp's unusual behavior. Another possible explanation is the abundance of tettigoniids. No abnormal behavior in prey transport and storage was observed, except that one *Scudderia* was abandoned at the nest entrance; the nest was subsequently filled with Acrididae. Each of the three other *Scudderia* was placed in a separate cell, together with two, five, and seven grasshoppers, respectively. No egg was laid on a tettigoniid, possibly because of their small size.

From three to nine prey are stored in a cell (Rau and Rau 1918; Kurczewski 1966*a*), their number being inversely proportional to their size (Strandtmann 1953). They are deposited head in, usually venter up, rarely dorsum up. The wasp's egg is laid across the prothoracic venter on one of the larger prey, usually the largest one. The larva consumes the provision in about a week, and the full developmental period from egg laying to adult emergence takes about two weeks in Texas (Strandtmann 1953).

Male behavior was studied by Kurczewski (1966*b*). The flight period begins and ends earlier in the season than the female's. The males fly rapidly but low over the ground, and land for short periods. As their number in an area increases, more of them appear to adhere rigidly to certain perches, such as stones, vegetation, pieces of wood and bark. Chasing or grappling occurs frequently (the resident usually pursues an intruder who has landed nearby). A male may perch motionless with raised forelegs, raised, rigid antennae, and the gastral tip touching (or nearly so) the sand surface. He may then pivot to the left or right, while keeping the gastral tip stationary. Open holes near their perches often attract his attention. Males spend the night, extremely hot periods, and inclement weather in shallow burrows

that they dig with mandibles and forelegs. Unlike the female, the male does not level the tumulus that accumulates at the burrow entrance. The burrow is closed off from within and has no apical cell. He stays at the end of the burrow, his head toward the entrance.

Copulation takes place on the ground and lasts for 25–35 seconds (Kurczewski 1966*b*). The male mounts the female, his wings folded flat over the dorsum. Nesting females usually resist males' attempts to mate.

Phrosinella aurifacies Downes, *Senotainia trilineata* (van der Wulp), and *S. vigilans* Allen (Diptera: Sarcophagidae) are cleptoparasites of *terminatus* (Spofford et al. 1986). Females of *Phrosinella aurifacies* fly in search of wasp nests (they investigate disturbed sand) and larviposit in the nest's entrance. Females of *Senotainia trilineata* maintain surveillance perches and pursue wasps carrying prey in the air (occasionally making contact in midair) or on the ground, but pay no attention to unattended prey. Females of *Senotainia vigilans* are attracted to provisioning or digging wasps (they remain near the nest until the wasp returns with prey); they larviposit on the prey while the wasp opens or enters the nest, inside the burrow, or in the entrance. Wasps try to evade pursuing flies, chase them off, or abandon their prey; they also clean maggots off the prey. *Perilampus hyalinus* Say (Hymenoptera: Perilampidae) parasitizes (Spofford and Kurczewski 1984) the two *Senotainia* that develop on the prey of *terminatus*.

Geographic Distribution (Fig. 115).—Widespread in North America, but absent from southern Florida, and west of 110th meridian. The species ranges from southern Manitoba and Prince Edward Island to El Salvador, and there are records from northern Colombia and the Roraima Territory in Brazil. It is largely replaced by *alpestris* west of the Rocky Mountains.

Material Examined.—954♀, 763♂.

Records.—CANADA: **Alberta:** Medicine Hat. **Manitoba:** Aweme, 5 mi W Carberry, 2 mi W Stockton. **Nova Scotia:** Halifax Co.: Cape Breton Highlands National Park, Lawrencetown. **Ontario:** Belleville, Brighton, Merivale near Ottawa, Ottawa, Point Pelee, Spencerville, Toronto. **Prince Edward Island:** Alberton, Brackley Beach, Dalvay House (P.E.I. National Park). **Quebec:** Hull, Joliette, Kazabazua, Lakeside, Lanoraie, Saint Hilaire, Tadoussac.

UNITED STATES: ALABAMA: **Clarke:** Thomasville. **Montgomery:** Montgomery. ARIZONA: **Cochise. Mohave:** Bullhead, Wikieup. **Pima:** Box Canyon, Sabino Canyon, Sahuarita. **Santa Cruz:** Nogales (also 10 mi NW), Sycamore Canyon (31°25'N, 111°12'W). **Yavapai:** Dewey. ARKANSAS: **Craighead:** Brookland. **Lafayette:** Lewisville. COLORADO: **Bent:** 2 mi S Hasty, 2 mi S Las Animas. **Boulder:** Boulder. **Cheyenne:** Aroya. **Crowley:** Ordway. **Larimer:** 14 mi N Fort Collins, Hewlett Gulch. **Logan:** Crook. **Mineral:** Creede. **Prowers:** Carlton. **Weld:** 1 mi NE Roggen. CONNECTICUT: **Hartford:** Hartford. **Middlesex:** Old Saybrook. **New Haven:** Haven. DISTRICT OF COLUMBIA: Washington. FLORIDA: **Alachua:** Gainesville (1♀, 6 June 1976, W. H. Pierce; UCD). **Gadsden:** Quincy. GEORGIA: **Chatham:** Savannah. **Clarke:** Athens, Whitehall Forest. **Decatur:** Bainbridge. **De Kalb:** Stone Mt. **Fulton:** Atlanta, Silver Lake. **Richmond:** Fort Gordon. **Thomas:** Ochlocknee. ILLINOIS: **Jackson:** Grand Tower. **Kane:** near Camp Big Timber. **Kankakee, Lake:** —. **Macoupin:** Carlinville. **McHenry:** Algonquin, McHenry. **Mason:** Havana, Sand Ridge State Forest. **Morgan:** Meredosia. **Peoria:** Peoria. **Williamson:** Crab Orchard Lake. INDIANA: **Knox:** Vincennes. **Tippecanoe:** Lafayette. IOWA: **Story:** Ames, 4 mi N Gilbert. **Woodbury:** Sargeant Bluff, Sioux City. KANSAS: **Atchison, Barton, Clay, Graham, Meade, Ness, Osborne, Phillips, Russell, Smith:** —. **Douglas:** Lawrence (also 5 mi NW). **Ford:** Dodge City. **Hamilton:** 2.5 mi S Kendall. **Kearny:** Lakin (also 9–13 mi S). **Kiowa:** Belvidere. **Ottawa:** 5 mi N Bennington. **Pottawatomie:** Blackjack Creek, 6 mi W Wamego. **Reno:** Pretty Prairie. **Riley:** Manhattan. MAINE: **Cumberland:** Portland. **Lincoln:** —. MARYLAND: **Anne Arundel:** Odenton. **Calvert:** —. **Prince Georges:** Beltsville, Laurel. MASSACHUSETTS: **Barnstable. Essex:** Andover. **Hampden:** Springfield. **Middlesex:** Bedford, Chelmsford, Lexington. **Nantucket:** Nantucket Island. **Norfolk:** Needham. **Suffolk:** Boston. MICHIGAN: **Alger:** —. **Berrien:** E. K. Warren State Park. **Clinton:** Rose Lake W. E. S. **Emmet:** Sturgeon Bay. **Livingston:** E. S. George Reserve. **Marquette:** Huron Mountain Club, Muskegon State Park. **Washtenaw:** Ann Arbor, Pinckney State Park on Half Moon Lake. **Wayne:** Detroit, Palmer Point. **Crawford, Kalkaska, Mecosta, Oakland:** —. MINNESOTA: **Anoka:** Fridley Sand Dunes. **Blue Earth:** Mankato. **Houston:** La Crescent **Koochiching:** —. **Lesueur:** Blakeley. **Nicolett:** Courtland. **Ramsey:** —. **Renville:** Olivia. **Sherburne:** —. MISSISSIPPI: **Monroe:** Aberdeen. MISSOURI: **Boone:** Columbia. **St. Louis City:** St. Louis. MONTANA: **Dawson:** Glendive. NEBRASKA: **Cuming:** West Point. **Dawson:** Cozad. **Douglas:** Omaha. **Fillmore:** Fairmont. **Hooker:** 1.5 mi N Mullen. **Kearney:** Kearney. **Morrill:** Bridgeport. **Sioux:** Glen. **Thomas:** Halsey, Thedford. NEW HAMPSHIRE: **Belknap:** Gilford–Alton. **Grafton:** Franconia, Hanover, White Mts. **Rockingham:** Hampton, Wentworth near New Castle. NEW JERSEY: **Atlantic:** Weymouth. **Burlington:** Browns Mills, Chatsworth, Lebanon State Forest. **Camden:** Clementon. **Cape May:** Reeds Beach, Stone Harbor. **Cumberland:** Vineland. **Gloucester:** Glassboro, North Woodbury, Westville. **Monmouth:** Freehold, Ocean Township, Tinton Falls. **Ocean:** Lakehurst, Lakewood. NEW MEXICO: **Bernalillo:** Albuquerque. **Grant:** —. **De Baca:** Sumner Lake State Park. **Guadalupe:** Santa Rosa. **Hidalgo:** 15 mi S Animas, Rodeo. **Lincoln:** Devils Canyon (20 mi NE Ruidoso). **Luna:** Deming. **Quay:** Tucumcari, Ute Lake State Park. **Socorro:** 4 mi W Abo State Monument, La Joya (20 mi N Socorro). **Roosevelt:** Oasis State Park, Portales. NEW YORK: **Albany:** Albany, Colonie, 2 mi S Rensselaerville. **Cayuga:** Auburn, Fair Haven, Union Springs. **Fulton:** Broadalbin. **Madison:** Chittenango, Hamilton. **Monroe:** Rochester. **New York City:** Pelham Park. **Oswego. Otsego:** East Worcester. **Putnam:** Brewster. **Richmond:** Staten Island. **Rockland:** Nyack. **Suffolk. Sullivan:** Beaver Kill. **Tompkins:** Groton, Ithaca, Ringwood. **Wayne:** —. NORTH CAROLINA **Brunswick:** Long Beach. **Dare:** Kill Devil Hills, Nags Head. **Macon:** Highlands. **Moore:** Southern Pines. **New Hanover:** Carolina Beach. **Onslow:** Onslow Beach. **Pender:** Surf City. **Wake:** Raleigh. NORTH DAKOTA: **Golden Valley:** Beach. **Ransom:** Sheldon (also 7 mi NE). **Richland:** 11 and 13 mi W Walcott. OHIO: **Franklin:** Columbus. OKLAHOMA: **Beaver:** Beaver State Park. **Cimarron:** Black Mesa State Park. **Marshall:** Lake Texoma (2 mi E Willis). **Tulsa:** Tulsa. PENNSYLVANIA: **Alleghany:** Natrona. **Erie:** Presque Isle State Park. **Huntingdon:** Turkey Run State Park. **Lehigh:** Lehigh Gap. **Philadelphia:** Philadelphia. **Westmoreland:** Jeannette. SOUTH CAROLINA: **Allendale:** Fairfax. **Georgetown:** 6 mi SSW Murrells Inlet. **Horry:** Myrtle Beach. TENNESSEE: **Knox:** —. **Shelby:** Memphis. TEXAS: **Atascosa:** Lytle. **Austin:** St. Austin State Park near Sealy. **Bexar:** —. **Bosque:** Valley Mills. **Brazos:** College Station. **Brewster:** Rio Grande. **Brooks:** 8 mi E Encino. **Comal:** New Braunfels. **Dallam:** Conlen. **Galveston:** Galveston. **Hidalgo:** Bentsen Rio Grande Valley State Park, McAllen Botanical Garden. **Jim Wells:** Palito Blanco. **Kenedy:** 3 mi S Sarita, Risken Ranch (27°10'N, 97°40'W). **Kimble:** Junction. **Kleberg:** Kingsville, Baffin Bay 20 mi SE Kingsville. **Lee:** Fedor. **Llano:** 11 mi E Llano. **Newton:** Sabina River at Highway 190. **Potter:** 5 mi N Amarillo. **Randall:** Palo Duro Canyon. **Refugio:** Bayside. **San Patricio:** Aransas River 10 mi NE Sinton, Chiltipin Creek at routes 77 and 181, Welder Wildlife Refuge (7 mi NE Sinton). **Starr:** Rio Grande City. **Travis:** Austin. **Uvalde:** Nueces River. **Webb:** 23 mi W Freer. **Wharton:** Wharton. **Wilson:** Floresville. VERMONT: **Orange:** Strafford, Union Village. VIRGINIA: **Alleghany:** Clifton Forge **Arlington:** Arlington, Glencarlyn. **Fairfax. Loudoun:** —. **Montgomery:** Westmoreland. **Norfolk:** Dismal Swamp. **Westmoreland:** Westmoreland State Park WISCONSIN: **Chippewa:** Stanley. **Dane:** Madison. **Grant:** Rutledge. **Milwaukee:** Milwaukee. **Pierce:** Maiden Rock, Prescott. **St. Croix:** N of Hudson. **Vernon:** Genoa

MEXICO: **Chiapas:** Montebello National Park. **Chihuahua:** 35 mi N Chihuahua, 11 mi W Gran Morelos, Hidalgo del Parral (also 9 mi S), 10 mi N Jimenez, 2 km W San Pablo Balleza (which is 26°57'N, 106°21'W). **Durango:** 10 mi W Durango, Nombre de Díos (23°51'N, 104°14'W). **Guanajuato:** 10 mi N Silao **Jalisco:** Atenguillo (65 km SSW Ameca), Estanzuela (40 km W Ameca), Guadalajara, Plan de Barrancas. **Mexico:** Tepexpan. **Michoacan:** Ciudad Hidalgo. **Morelos:** Yautepec. **Nayarit:** Playa Matanchen near San Blas. **Oaxaca:** 10 mi SE Tepanatepec. **San Luis Potosi:** El Naranjo–El Salto. **Sinaloa:** 2.5 mi N Mazatlán, 20 mi E Villa Unión. **Sonora:** Magdalena, Río Chuchajachi (7 mi S Alamos), E Yaqui River (35 air km WSW Sahuaripa), 15–25 km NW Yecora. **Tamaulipas:** Matamoros, Municipio de Aldama (Rancho Nuevo), Rio Blanco (18 mi N Ciudad Victoria). **Tlaxcala:** 10 mi N Apizaco. **Veracruz:** Fortín de las Flores. **Zacatecas:** 2 km SW Valparaiso

CENTRAL AND SOUTH AMERICA (some South American records are not shown on Fig. 115): BRAZIL: **Roraima Territory:** Surumú. COLOMBIA: **Guajira:** Riohacha. **Valle del Cauca:** Cali. **Tolima:** Armero. EL SALVADOR. Quezaltepeque. GUATEMALA: near Guatemala, Lago de Atitlán. VENEZUELA: **Valle:** Loboguerrera. **Zulia:** Rosario

FIGURE 115. Geographic distribution of *Tachysphex alpestris* Rohwer, *quisqueyus* sp. n., and *terminatus* (F. Smith).

Tachysphex similis Rohwer

(Figures 115, 117)

Tachysphex similis Rohwer, 1910:51, ♀, ♂. ! Lectotype: ♀, Texas: Lee Co.: Fedor (USNM), present designation.—J. Smith 1910:683; Krombein 1950:267; Wray 1950:38; G. Bohart 1951:952; Krombein 1951:143, 1952:93, 1953*a*:330, 1953*b*: 122, 132; Krombein and Evans 1954:232, 1955:231; Krombein 1958*c*:188, 1963*b*:273, 1964:15; Kurczewski 1966*b*:436–453; Krombein 1967:393; Kurczewski 1967:279, 1971:114 (in key); Wray 1967:123; Elliott and Kurczewski 1974:725; Bohart and Menke 1976:276; Krombein 1979:1631; Finnamore 1982: 104; Elliott and Kurczewski 1985:295.

Tachysphex simulans Rohwer, 1910:52, ♀. ! Holotype: ♀, Texas: Lee Co.: Fedor (USNM). Synonymized by G. Bohart 1951:952.

Tachysphex terminatus: Krombein 1953*c*:13 (!).

Diagnosis.—*Tachysphex similis* has a toothlike prespiracular prominence on the upper metapleuron (Fig. 116b–d), the posterior margin of the prominence being approximately as long as the anterior one. In most specimens, the prominence is sharper than in other species (*apicalis, terminatus*) that have a similar structure. The female can also be recognized by an unevenly microrugose frons with ill-defined punctures (Fig. 116a) combined with a narrow vertex (width 1.4–1.7× length). The male differs from *apicalis* in having a well-developed foretarsal rake, and from *terminatus* by the characters discussed under that species.

Description.—Frons unevenly microrugose, with ill-defined punctures (Fig. 116a) that are totally reduced in some specimens. Scutal punctures, in most specimens, less than one diameter apart adjacent to margins and around admedian lines, but one to three diameters apart in remaining U-shaped area; all punctures about one diameter apart or less in many individuals. Upper metapleuron (Fig. 116b–d): flange broad, oblique carina beneath its anterior end becoming higher toward flange but abruptly lowered at its attachment; prespiracular prominence conspicuous, consisting of three carinae (anterior, posterior, and admedian one) which have a common apex; anterior and posterior carinae about equal in length; prominence acutely angulate in most females and many males. Propodeum finely sculptured between dorsum and side. Basal tooth of hindcoxa large in most specimens.

Vestiture partly obscuring sculpture between antennal socket and orbit.

♀.—Width of clypeus 2.4–2.8× length; bevel shorter than basal area; lip arcuate, without median projection. Vertex width 1.4–1.7× length. Dorsal length of flagellomere I 1.5–1.9× apical width. Length 6.0–9.5 mm.

Setal length about 1.7 MOD on vertex and about 1.0 MOD on scutum anterolaterally.

Gaster usually black, but occasionally one or two apical segments yellowish red (specimens with red gastral tip are frequent in Lawrence and Manhattan, Kansas; Kenedy, Kleberg, and Lee counties, Texas; and in Nebraska). Terga I–IV silvery fasciate apically.

♂.—Width of clypeus 2.2–2.7× length; lip corners equidistant from antennal socket and one another. Vertex width 1.6–2.2× length. Outer apical spine of foretarsomere II sometimes only two-thirds length of tarsomere III, but even then distinctly longer than corresponding inner spine. Length 4.4–6.2 mm.

Setal length about 1.3 MOD on vertex and 1.0 MOD on scutum anterolaterally.

Gaster usually black, but segment VII red in some specimens from Kansas and Fedor, Texas, and also in occasional specimens from Florida and New Jersey. Gastral terga I–IV or I–V silvery fasciate apically.

Variation.—The mesopleural punctures are about one diameter apart in most specimens. They average two diameters apart in two females from Eleuthera Island, Bahamas (AMNH, FSCA), but are the usual distance apart in the seven males from that island (CAS, FSCA).

Elliott and Kurczewski (1974) found size displacement in mixed colonies of *similis* and *terminatus*. See the latter species for details.

Life History.—Krombein (1951) observed individuals feeding on tulip-tree honeydew produced by *Toumeyella liriodendri* (Gmel.), and also (1953*a*) visiting foliage of *Quercus marilandica* Muench. When digging a nest, the female works with both forelegs moving synchronously (Krombein 1964). She levels the sand that accumulates at the nest entrance. The nest may be 7.5 cm long, with the lower end 3–6 cm below the soil surface (the burrow is oblique to the soil surface). Krombein recorded two or three cells per nest, but Elliott and Kurczewski (1985) observed one and four. The burrow is temporarily closed during the provisioning period. The known prey consists of young grasshopper nymphs of *Radinotatum* sp. (Krombein and Evans 1955), *Aptenopedes* sp., and *Melanoplus* sp. (Krombein 1964), and also *Melanoplus* sp., *Mermeria* sp., *Opeia obscura* (Thomas), and *Pseudopomala brachyptera* (Scudder) according to Elliott and Kurczewski (1985). Two females studied are pinned with prey: one from Marco, Florida (AMNH), with a juvenile *Schistocerca* sp., det. A. B. Gurney, and one from St. Catherine Island, Georgia (UGA) with a nymph of *Melanoplus devastator* Scudder, det. D. C. F. Rentz. The prey may be flown or transported on the ground. It is held venter up, the wasp's mandibles grasping the antennal bases. Prey is deposited about 1 cm from the nest entrance; the female then opens the temporary closure, enters the nest, turns around inside, emerges headfirst, grasps the grasshopper, and pulls it inside. From 4 to 10 prey, 5–8 mm long, may be stored in a cell (Krombein 1964), but Elliott and Kurczewski (1985) observed 3 and 5 prey per cell. The only egg observed was laid across the venter of the largest prey between the fore- and midcoxae.

The male behavior (Kurczewski 1966*b*) is as described for *terminatus* (see that species), with a few minor differences.

Geographic Distribution (Fig. 117).—United States and Canada east of the Rocky Mountains (also Colorado, Utah, and southern Alberta), north to New Brunswick and Northwest Territories; and south to Minatitlán, Mexico; also Bahama Islands.

Material Examined.—1,092♀, 532♂.

Records.—CANADA: **Alberta:** Medicine Hat, 12 km SW Orion, Writing-on-Stone Provincial Park. **Manitoba:** Aweme, Brandon, 5 mi W Carberry, 2 mi W Stockton. **New Brunswick:** Shediac. **Northwest Territories:** Rae. **Ontario:** Belleville, Fort Erie, Kearney, Ontario, Strathroy, Toronto. **Quebec:** Kazabazua, Lakeside, Lanoraie, St. Hilaire. **Saskatchewan:** Elbow, Moose Jaw (also 21 mi W).

UNITED STATES: ALABAMA: **Limestone:** Decatur. **Montgomery:** Montgomery. ARKANSAS: **Desha, Madison:** —. COLORADO: **Bent:** Hasty. **Boulder:** White Rocks near Boulder. **Costilla:** Ute Creek. **El Paso:** Colorado Springs. **Larimer:** Fort Collins. **Moffat:** Lay. **Morgan:** —. **Weld:** Owl Creek (11 mi NE Nunn). CONNECTICUT: **Tolland:** Vernon. DISTRICT OF COLUMBIA: Washington. FLORIDA: **Alachua. Brevard:** Cocoa, Titusville. **Broward:** Lauderdale, Seminole State Park. **Calhoun:** Blountstown. **Charlotte:** Bermont, Punta Gorda. **Clay:** Camp Crystal. **Collier:** Corkscrew Swamp Sanctuary, Everglades, Marco. **Dade:** Miami. **DeSoto:** Arcadia. **Duval:** Jacksonville, Millerton. **Gadsden:** Quincy. **Glades:** Palm-

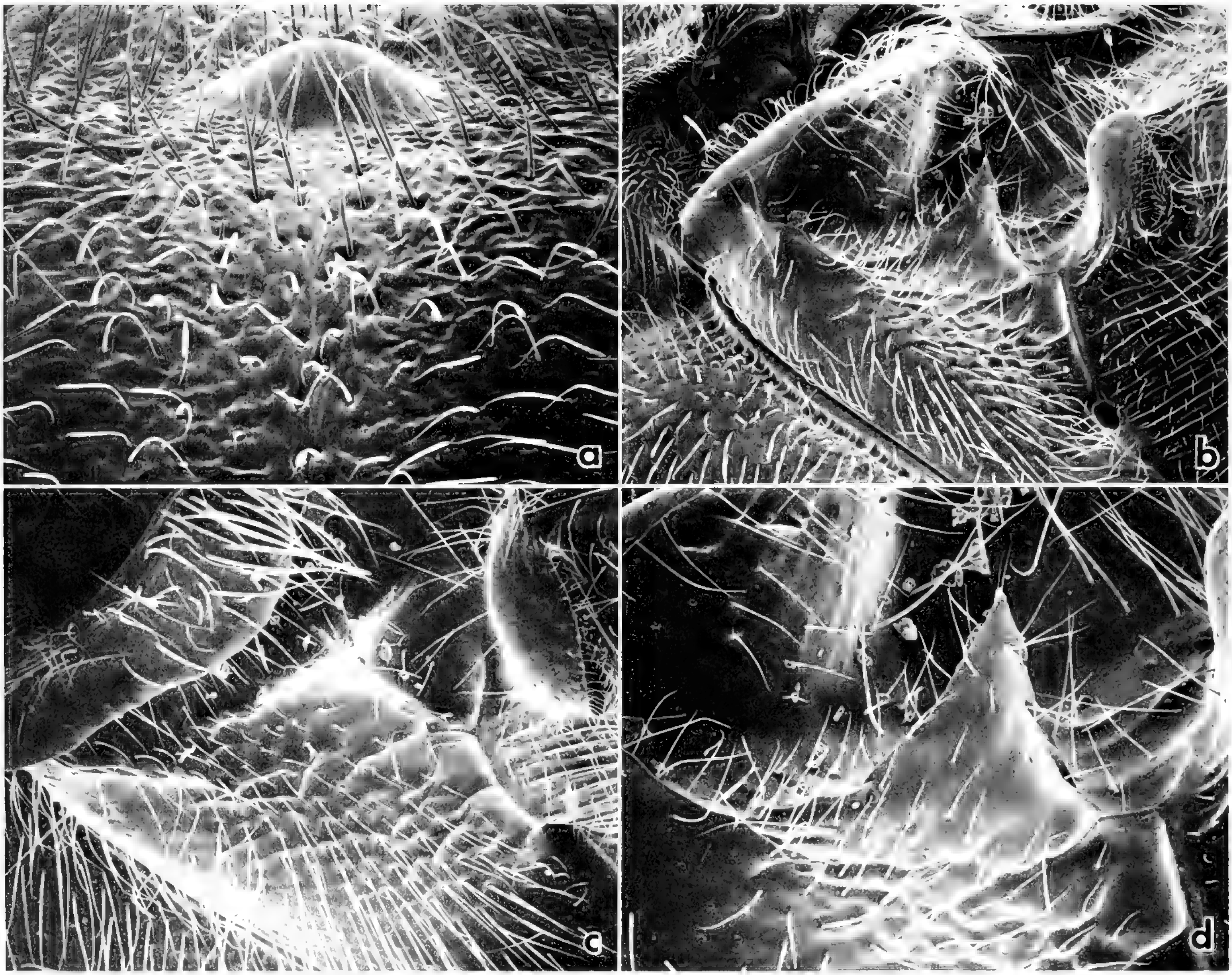

FIGURE 116. *Tachysphex similis* Rohwer, female: a—frons adjacent to midocellus, b—upper metapleuron, lateral view; c—same, top view; d—prespiracular prominence of upper metapleuron.

dale. **Gulf**: St. Joseph Peninsula. **Hendry**: LaBelle. **Highlands. Lake**: Leesburg. **Lee**: Olga, Fort Myers, Sannibel Island. **Leon**: Tall Timber Research Station. **Levy**: Cedar Key. **Liberty**: Apalachicola National Forest, Sumatra, Torreya State Park. **Manatee**: Bradetown. **Marion**: Eureka, Lake Eaton, 5 mi E Lynn. **Monroe**: Cape Sable, Key West. **Okaloosa**: 1.7 mi N Holt. **Orange**: Orlando, Vineland. **Pinellas**: Dunedin. **Polk**: Indian Lake Estates. **Putnam, Santa Rosa**: Blackwater River State Forest. **Sarasota**: —. **Suwannee**: Suwannee River State Park. **St. Lucie**: Fort Pierce. **Taylor**: Blue Spring Lake, Keaton Beach, 32 mi SE Perry. **Volusia**: Ormond Beach. **Wakulla**: Ochlockonee River State Park, 3 mi NW Sopchoppy. **Walton**: 2 mi E Mossy Head. GEORGIA: **Camden**: Cumberland Island. **Charlton**: Okefenoke Swamp. **Clarke**: Athens. **Decatur**: Springs Creek. **De Kalb**: Stone Mt. **Fulton**: Atlanta. **Glynn**: St. Simons Island. **Johnson**: near Kite. **Liberty**: St. Catherine's Island. **Marion**: Buena Vista. **Pike**: Zebulon. **Taylor**: Butler. **Tift**: Tifton. **White**: Cleveland. ILLINOIS: **Kankakee**: St. Anne. **Macoupin**: Carlinville. **Mason**: Havana, Sand Ridge State Forest. **Morgan**: Meredosia. IOWA: **Story**: Ames. **Woodbury**: Sioux City. KANSAS: **Barton**: —. **Dickinson**: Abilene. **Douglas**: Baldwin, Lawrence (also 5 mi NW). **Osborne, Phillips**: —. **Pottawatomie**: Blackjack Creek, Little Gobi Desert. **Reno**: Medora. **Riley**: Manhattan. **Stafford**: Salt Flats area. KENTUCKY: **Hardin**: Fort Knox. LOUISIANA: **East Feliciana**: 4 mi S Jackson. MAINE: **Penobscot**: Orono. MARYLAND: **Ann Arundel**: Odenton. **Montgomery**: Plummers Island. **Prince Georges**: Beltsville. MASSACHUSETTS: **Barnstable**: Woods Hole. **Hampden**: Springfield. **Middlesex**. MICHIGAN: **Alger**: Pictured Rocks National Lakeshore. **Allegan**: Allegan State Game Area. **Cheboygan**: Douglas Lake. **Emmet**: Douglas Lake. **Huron**: Sand Point. **Livingston**: E. S. George Reserve. **Marquette**: Huron Mountain Club. **St. Joseph**: Klinger Lake. **Washtenaw**: Ann Arbor, Pinckney State Recreation Area near Half Moon Lake. **Wayne**: Palmer Peak. **Cheboygan, Iosco, Otsego, Van Buren**: —. MINNESOTA: **Hennepin**: Minneapolis. **Kittson**: Lancaster. **Nicolett**: Courtland. **Olmsted**: —. MISSISSIPPI: **Harrison**: 10 mi N Biloxi. **Marshall**: Holly Springs. MISSOURI: **Boone**: Columbia. **Warren**: Warrenton. MONTANA: **Dawson**: Glendive. **Jefferson**: —. NEBRASKA: **Antelope**: Grove Lake. **Cherry**: 10 mi S Nenzel (on Niobrara River), Valentine National Wildlife Refuge. **Cuming**: West Point. **Dawes**: Chadron. **Hooker**: 1.5 mi N Mullen, 15 mi S Mullen (on Dismal River). **Lincoln**: North Platte. **Scotts Bluff**: Mitchell. **Sioux**: Sawbelly Canyon. **Thomas**: Halsey, Thedford. NEW HAMPSHIRE: **Belknap**: Meredith. **Grafton**: Compton. **Strafford**: Durham. NEW JERSEY: **Atlantic**: Weymouth. **Bergen**: Ramsey. **Burlington**: Lebanon State Forest, Vincentown. **Camden**: Hadden Heights. **Cape May**: 3 mi S Seaville. **Cumberland**: Vineland. **Gloucester**: North Woodbury, Pitman. **Monmouth**: Little Silver. **Ocean**: Lakehurst, 5 mi W Lakewood, Point Pleasant. **Union**: Westfield. NEW MEXICO: **Bernalillo**: Albuquerque. **Sandoval**: Jemez Springs. **Socorro**: La Joya (20 mi N Socorro). NEW YORK: **Cayuga**: Fair Haven. **Monroe**: Rochester. **Suffolk**: Cold Spring Harbor, Mattituck. **Westchester**: Ardsley. NORTH CAROLINA: **Cumberland**: Fort Bragg. **Dare**: Kill Devil Hills, Nags Head. **Moore**: Southern Pines. **Pamlico**: Havelock. **Wake**: Raleigh. NORTH DAKOTA: **Golden Valley**: Beach. **Ransom**: Sheldon. **Richland**: McLeod area, Walcott, 13 mi W Walcott. OHIO: **Mercer**: —. OKLAHOMA: **Beaver**: Beaver State Park. **Cimarron**: Black Mesa

FIGURE 117. Geographic distribution of *Tachysphex similis* Rohwer.

State Park. **Marshall:** Lake Texoma (2 mi E Willis). SOUTH CAROLINA: **Aiken:** Aiken. **Beaufort:** Hilton Head Island. **Charleston:** Dewees Island. TEXAS: **Anderson:** Salmon. **Atascosa:** Pleasonton. **Bastrop:** 6 mi E Bastrop. **Bell:** Holland. **Caldwell:** Luling. **Duval:** 8 mi W Premont. **El Paso:** El Paso. **Galveston:** Galveston. **Gonzales:** Palmetto State Park. **Karnes:** Gillett. **Kenedy:** Risken Ranch (27°10′N, 97°40′E), Sarita. **Kleberg:** Kingsville, 6 mi E Riviera (=Baffin Bay 20 mi SE Kingsville). **Lee:** Fedor. **Nueces:** Padre Island. **Potter:** 5 mi N Amarillo. **Randall:** Palo Duro Canyon State Park. **Sabine:** 6 mi NW Hemphill. **San Patrizio:** 10 mi NE Sinton on Aransas River. **Waller:** Stephen Austin State Park near Sealy. UTAH: **Cache:** Cornish. **Duchesne:** Roosevelt. **Uintah:** SW Bonanza, Green River 5 mi NE Jensen. VIRGINIA: **Arlington:** Arlington. **Fairfax:** Dunn Loring near Vienna, Falls Church, Great Falls. **Westmoreland:** Westmoreland State Park. WISCONSIN: **Grant:** Rutledge, Wyalusing. **Vernon:** Genoa. **Washington:** West Bend.

MEXICO: **Veracruz:** Minatitlán

BAHAMA ISLANDS: **Eleuthera Island:** Government Harbor's, Rainbow Bay **San Salvador Island:** –

Tachysphex apicalis W. Fox

(Figures 118, 119)

Tachysphex apicalis W. Fox, 1893:53, ♀, ♂. ! Lectotype: ♀, southern Florida: no specific locality (ANSP), designated by Cresson 1928:43.—W. Fox 1894*a*:521; Dalla Torre 1897:678, Ashmead 1899:250, Rohwer 1916:687; Britton 1920 340; Brimley 1938:443; G. Bohart 1951:950; Krombein and Evans 1954:232, 1955:321; Evans 1964:288; Krombein 1964:15, Kurczewski 1966*b*:436; Krombein 1967:392, Kurczewski and Snyder 1968:30, 31; Kurczewski 1971:114 (in key); Pulawski 1974*a*:48; Bohart and Menke 1976:272; Rust et al. 1985:46; Parks 1986:34.—As *apicalis apicalis*: Pulawski *in* Krombein 1979:1630

Tachysphex fumipennis W. Fox, 1894*a*:518, ♀. ! Lectotype: ♀, Florida: St. John's Co.: near St. Augustine (ANSP), designated by Cresson 1928:44. Synonymized by G. Bohart 1951:950.—Dalla Torre 1897:680, Ashmead 1899:250 (as *fuscipennis*)

Tachysphex fusus W. Fox, 1894*a*:519, ♀, ♂. ! Lectotype: ♂, Texas: no specific locality (ANSP), designated by Cresson 1928:44.—Dalla Torre 1897:680, Ashmead 1899:250, Cockerell 1900 144; Williams 1914:172, 201; Rohwer 1916:687 (as *fuscus*); Stevens 1917:422, Mickel 1918:422, Rau and Rau 1918:149 (as *fuscus*), Williams 1931:239, 1932:17; Brimley 1938:443, Williams 1940:367; Fullaway and Krauss 1945:36 (as *fuscus*); Strickland 1947:129 (as *fuscus*); G. Bohart 1951 951, Yoshimoto 1960:331 (as *fuscus*), Krombein 1967:393; Kurczewski and Snyder 1968:30, 31; Bohart and Menke 1976:274.—As *apicalis fusus*: Pulawski *in* Krombein 1979:1630, Rust et al. 1983:406; Elliott and Kurczewski 1985 294

Tachysphex foxii Rohwer, 1908:222, ♂. ! Holotype: ♂, Colorado: Boulder Co Boulder (USNM). Synonymized with *fusus* by G. Bohart 1951:951

Diagnosis.—The following combination of characters distinguishes *apicalis*: clypeus narrow, its width 2.0–2.5 × length (Fig. 118a, b, f); frons shiny, frontal punctures in most specimens well defined (Fig. 118c); upper metapleuron with an angulate prespiracular prominence. The female clypeal lip has a small, median projection (Fig. 118b), also found in *antillarum*, *ruficaudis*, and some *terminatus*. The foretarsal rake is absent in most males (as it is in *ruficaudis*, some *linsleyi*, and the extralimital *galapagensis*). A rudimentary or fully developed rake is present in some males from the southeastern United States, but in specimens from this area (both sexes) the propodeum is coarsely sculptured between dorsum and side (Fig. 118e). This type of sculpture is shared with many *ruficaudis*.

Description.—Frons shiny, with well-defined punctures (Fig. 118c) except in occasional western specimens. Scutal punctures less than one diameter apart adjacent to margins and around admedian lines, but two or three to several diameters apart in remaining U-shaped area. Metapleural flange broad; upper metapleuron with prominence before propodeal spiracle (which is very small in some specimens from Nevada and California); prominence consisting of three carinae (anterior, posterior, and admedian) which have a common apex; anterior and posterior carinae about equal in length; oblique carina beneath anterior end of flange becoming higher toward flange, but abruptly lowered at its attachment. Hindcoxa with prominent basal tooth.

Sculpture not obscured or only partly obscured by vestiture between antennal socket and orbit.

♀.—Clypeus width 2.0–2.5 × length (Fig. 118a, b). Vertex width 1.8–2.3 × length. Setal length about 2.0 MOD on vertex, varying geographically on scutum.

♂.—Clypeus 2.1–2.3 × wider than long; lip arcuate, its corners obtuse to rectangular, slightly closer to each other than to antennal socket (Fig. 118f). Vertex width 2.1–2.6 × length. Sterna II–IV glabrous posteriorly. Setal length about 2.0–2.3 MOD on vertex, about 2.0 MOD on scutum.

Geographic Variation.—Over its range, *apicalis* has several forms which differ mainly in the propodeal sculpture and color of wings. These forms intergrade as given below:

1) The commonest and widespread form occurs throughout North and Central America but is absent from southeastern United States. It is characterized by a fine sculpture between the propodeal dorsum and side (Fig. 118d), and by the hyaline to weakly infumate wings. Setae about 2.0 MOD long anterolaterally on scutum. Female features are: clypeus 2.2–2.5 × wider than long; lip with one or three weak, obtuse projections; dorsal length of flagellomere I 2.0–2.4 × apical width; vertex width sometimes clearly more than twice length; length 7.0–9.5 mm; gaster with one or two apical segments red; terga I–IV (rarely I–V) silvery fasciate apically. Male features are: foretarsal rake absent; outer apical spine of foretarsomere II about as long as corresponding inner spine; length 5–8 mm; terga I–IV silvery fasciate apically.

2) Specimens from the southeastern United States (Washington, D.C., south to Florida) differ as follows: the propodeum is coarsely sculptured between the dorsum and side (Fig. 118e), and the wings, especially in the female, are infumate. Female features are: clypeus 2.0–2.3 × wider than long; lip with small, obtuse, median projection; dorsal length of flagellomere I 1.9–2.0 × apical width; length 8–10 mm; setal length 1.0 MOD (Florida) to 2.0 MOD (Washington, D.C.) anterolaterally on scutum; gaster black, segment VI usually red; terga I–III (Florida) or I–IV (Washington, D.C.) silvery fasciate apically. Male features are: foretarsal rake absent or rudimentary, but well developed in a male from Indian Lake Estate, Florida (UGA), in which there are five preapical rakes, and four of them are longer than basitarsal width; outer apical spine of foretarsomere II equal to or longer than corresponding inner spine; length 6.5–8.0 mm; setae length varying from about 1.0 to about 2.0 MOD anterolaterally on scutum; gaster black, two apical segments often reddish; terga I–III or I–IV silvery fasciate apically.

This is the nominotypical form of *Tachysphex apicalis* W. Fox.

3) Specimens from Nerinx, Kentucky (1♀, 3♂, USNM), and Santuc, South Carolina (1♀, UCD), display propodeal sculpture that is intermediate between forms 1 and 2, and their wings are weakly infumate. In the following females the propodeal sculpture is weak (as in the main continental form), but the wings are almost as dark as in the southeastern United States: one from Greenville, South Carolina (HKT), one from Kennesaw Mt., Georgia (UGA), and one from Warren Dunes State Park, Michigan (MOB). Specimens from the following localities are intermediate both in sculpture and wing color: Lehigh Gap, Pennsylvania (2♀, ANSP); North Woodbury, New Jersey (1♀,

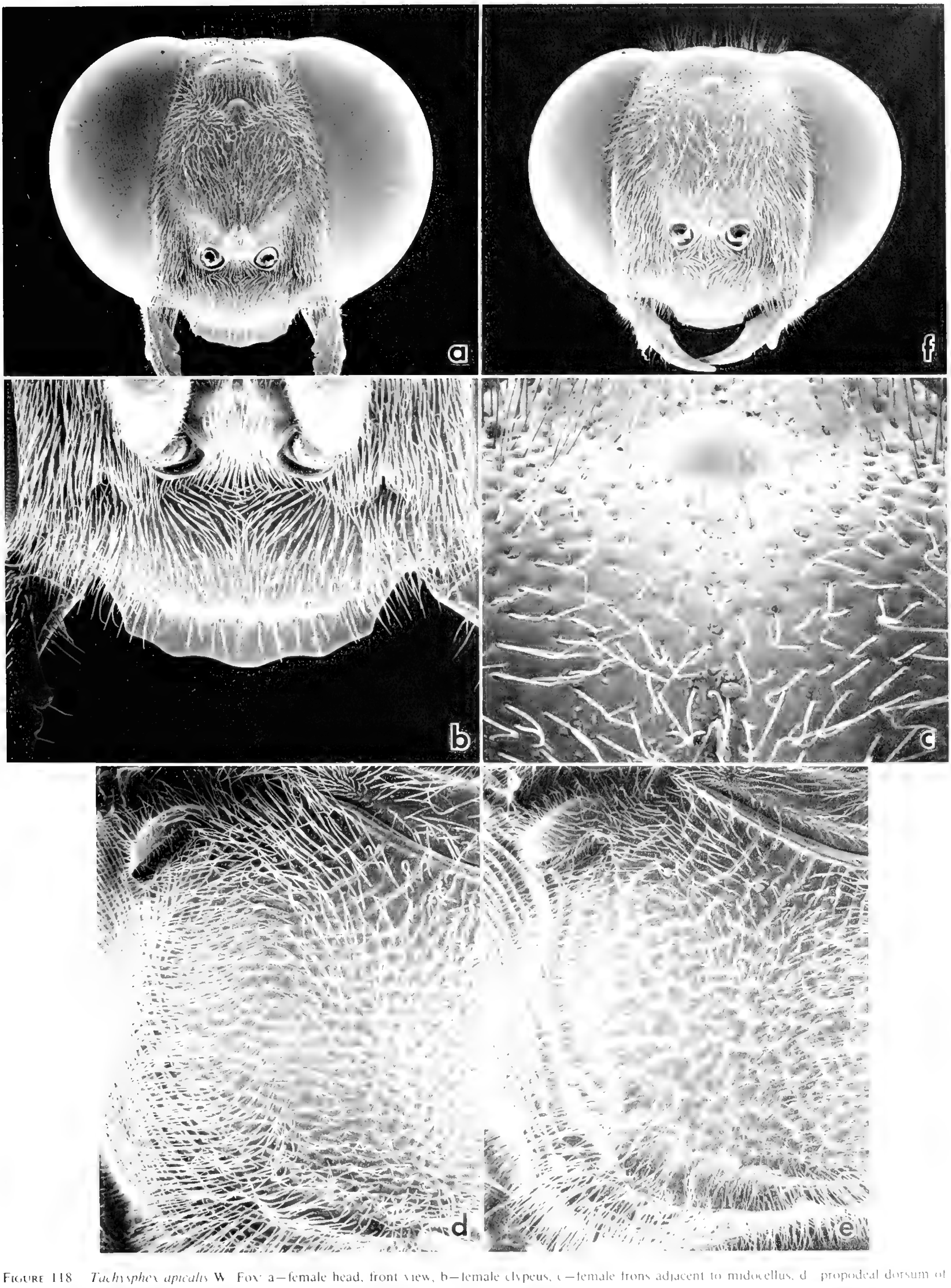

FIGURE 118 *Tachysphex apicalis* W. Fox: a—female head, front view, b—female clypeus, c—female frons adjacent to midocellus, d—propodeal dorsum of a western U.S. specimen, oblique view, e—same, Floridan specimen, f—male head, front view.

ANSP); Raleigh, North Carolina (2♀, CU, NCSU); Salisbury, North Carolina (1♀, NCSU); and Atlanta, Georgia (1♀, MCZ).

4) In Cuban specimens, the propodeal sculpture is coarse, as in the southeastern United States form, but the wings are hyaline, as in the main continental form (Pulawski 1974*a*). Also a female from El Camaron, Mexico (UCD), belongs here.

5) Hawaiian *apicalis* are morphologically identical to the main continental form, but their wings are slightly darker.

Life History.—The most striking biological property of *apicalis* is its habit of nesting in sloping banks or cliffs (Kurczewski and Snyder 1968), which may be several centimeters to many meters high. Rau and Rau (1918) recorded a female digging horizontally in an ant-lion pit, halfway down in the funnel, and I observed nests established in vertical parts of land tortoise holes (near their entrances) at the Archbold Biological Station, Florida, in April 1975. Rau and Rau (1918) observed a female digging in the mortar between the foundation rocks of an abandoned house, and Elliott and Kurczewski (1985) saw a female searching between siding shingles of a cottage.

As Kurczewski and Snyder (1968) pointed out, this unusual nest placement has further implications. First, the nest's gallery is horizontal rather than vertical (Krombein 1964). Second, the sand excavated from the burrow rolls down and cannot be reused for the nest closure. Hence, the nest remains open during the provisioning period, and the female returning with prey enters the burrow without pausing at the entrance. Only rarely, when an unusually large prey is brought in, does she stop inside the entrance and drop her prey. In this case the grasshopper is pulled inside in the manner described under *terminatus*. Third, for the final closure of the nest, sand from the sides and top of the burrow is used.

The nest has up to several cells, each filled with several prey. The prey consists of immature grasshoppers of many genera (Krombein 1967, no specific data). Williams (1914) recorded *Melanoplus* and Tryxalinae, and also *Oxya chinensis* (Thunberg) from Oahu, Hawaii (Williams 1932). Krombein (1964) found seven nymphs of a *Melanoplus*, possibly *puer* (Scudder), in a cell; they were 7–10 mm long. The egg was laid across the venter of a medium-sized nymph between the fore- and midcoxae. Elliott and Kurczewski (1985) examined an unfinished nest whose single cell contained seven nymphal acridids *Melanoplus sanguinipes* (Fabricius) and an eighth prey being carried by the female. The prey were placed head inward, venter up, or on the side.

Male behavior was studied by Kurczewski (1966*b*). The flight period begins and ends earlier in the season than the female's. After emergence males make frequent, very rapid flights back and forth in front of cliffs, landing periodically on the cliff. The perching posture is the same as in *terminatus* (see that species). Males spend the night in burrows in the cliff, but they were never observed digging. They probably use preexisting holes, as suggested by the fact that two or three males, or a male and a female, are sometimes found in the same burrow (their heads toward the entrance); another indication is that the foretarsal rake of the male is absent or rudimentary. As in *similis* and *terminatus* (see the latter species), the male frequents several perches. He also has been observed pouncing upon other males and chasing invaders that approach his perch. He may walk from his perch and explore an open hole. Unlike *similis* and *terminatus*, he often goes completely inside, turns around, and exits headfirst.

A female from Broadus, Montana (KU) was collected on flowers of *Helianthus petiolaris* Nutt.

Geographic Distribution (Fig. 119).—Transcontinental, north to Pennsylvania, Wisconsin, North Dakota, southern Alberta, and southern British Columbia, south to southern Mexico; also Cuba and introduced into the Hawaiian Islands.

The first Hawaiian specimen was taken at Waiane, Oahu, in 1931, and then a pair at Mount Kaala, Oahu, in 1939 (Williams 1931, 1932, 1940). Judging from the number of specimens preserved in various collections, *apicalis* was common at Pearl Harbor, Oahu, by 1947.

Material Examined.—Central and western form: 734♀, 828♂; southeastern form 227♀, 251♂ (AMNH, ANSP, CAS, CNC, CU, FSCA, LEM, MCZ, NYSU, UCD, UGA, UMMZ, USNM, USU, WSU). Hawaiian specimens: 7♀, 12♂ (CAS, CSDA, HKT, USNM, UW).

Records.—Records without reference in parentheses refer to form 1, main continental form; (se) refers to form 2, or the southeastern form; (i) refers to form 3, or the intermediates. CANADA: **Alberta:** Medicine Hat, 12 km SW Orion, Writing-on-Stone Provincial Park. **British Columbia:** Summerland.

UNITED STATES: ALABAMA: **Montgomery:** Montgomery. ARIZONA: **Apache:** Canyon de Chelly National Monument. **Cochise. Coconino:** Cameron. **Gila:** Globe, Salt River Canyon, San Carlos. **Graham:** 4 mi W Calva, Roper Lake State Park (6 mi S Safford). **Maricopa. Mohave. Navajo:** Snowflake. **Pima. Pinal:** 14 mi E Oracle, 3 mi W Superior (Boyce Thompson Arboretum). **Santa Cruz. Yavapai:** 1 mi SE Camp Verde, Prescott. **Yuma:** 3 mi W Aztec, 10 mi N Ehrenberg, Yuma (also 30 mi NE). ARKANSAS: **Conway:** —. CALIFORNIA: **Alameda:** Niles Canyon, Sycamore Grove State Park (3 mi S Livermore), Tesla Road. **Alpine:** Silver Creek. **Colusa:** Colusa. **Contra Costa. El Dorado:** Snowline Camp. **Fresno:** Warthan Canyon, 8 mi NW Coalinga. **Glenn:** Hamilton City. **Imperial. Inyo. Kern:** Antelope Canyon near Tehachapi, Maricopa, 7.3 mi E Weldon. **Lassen:** Hallelujah Junction, Wendel. **Los Angeles. Modoc:** Fort Bidwell. **Mono. Monterey:** Arroyo Seco, Paraiso Springs. **Napa:** Samuel Springs (now bottom of Lake Berryessa). **Nevada:** Boca. **Orange:** Crystal Beach, Irvine Park, Santa Ana. **Placer. Riverside. Sacramento:** 2 mi E Fair Oaks, Folsom, Sacramento. **San Benito:** New Idria Road 4 mi SW Junction Panoche Road. **San Bernardino. San Diego. San Mateo:** Redwood City. **Santa Barbara:** including Santa Cruz Island. **Santa Clara:** Palo Alto. **Santa Cruz:** —. **Shasta:** Cassel, Redding, 2 mi W Shingletown. **Solano:** 8 mi W Winters. **Sonoma:** Healdsburg, Maacama Creek. **Stanislaus:** Del Puerto Canyon, Knight's Ferry. **Trinity:** Junction City. **Tulare:** Kennedy Meadow. **Ventura:** Oxnard, Wagon Road No. 2 Campground (18 air mi WSW Gorman). **Yolo:** Davis, Elkhorn Ferry, Rumsey, opposite Sacramento. COLORADO: **Alamosa:** Great Sand Dunes. **Boulder:** Boulder. **Chaffee:** Buena Vista. **Crowley:** Olney Springs. **Eagle:** State Bridge near Bond. **Larimer. Mesa:** Colorado River S Loma. **Moffat:** Sunbeam. **Montezuma:** 3 mi W Arriola. **Weld:** Owl Creek (12 mi NE Nunn), 1 mi NE Roggen. DISTRICT OF COLUMBIA: Washington (partly se). FLORIDA (se): **Alachua:** Gainesville, Monteoca (11 mi NW Gainesville). **Bradford:** —. **Brevard:** Cocoa. **Broward:** Hollywood. **Clay:** Camp Crystal. **Collier:** Corkscrew Swamp Sanctuary. **Dade:** Miami. **DeSoto:** Arcadia. **Duval:** Jacksonville. **Glades:** Lakeport. **Gulf:** Port St. Joe. **Hendry:** Devil's Garden (23 mi SW Clewiston). **Highlands:** Lake Placid, Sebring, Venus. **Lee:** Sanibel Island. **Levy:** Cedar Key. **Marion:** 9 mi SSW Ocala, Ocala National Forest. **Monroe:** Fleming Key. **Orange:** Orlando, Winter Park. **Osceola:** Kissimee. **Polk:** Indian Lake Estates. **Putnam:** Georgetown, 2 mi NW Orange Springs, Red Water Lake, Welaka. **St. John's:** St. Augustine. **St. Lucie:** Fort Pierce. **Santa Rosa:** —. GEORGIA: **Decatur:** Bainbridge (se). **Fulton:** Atlanta (i). **Liberty:** St. Catherine's Island (se). **Richmond:** Fort Gordon (se). **Tift:** Tifton (se). HAWAII: **Oahu:** Mt. Kaala (Williams 1940), Pearl Harbor, Waiane (Williams 1931, 1932). IDAHO: **Ada:** Lucky Peak Reservation. **Canyon:** 2 mi N Melba, Murphy. **Cassia:** Murtaugh. **Elmore:** 3.9 mi W Hamett, Mayfield, 16 mi SW Mountain Home, Mountain Home Air Base. **Franklin:** 12 mi NE Preston, Weston Canyon. **Fremont:** St. Anthony, St. Anthony Sand Dunes. **Gooding:** 1 mi NE Gooding. **Lemhi:** 9 mi N Ellis. **Nez Perce:** Central Grade, Lewiston. **Oneida:** Black Pine Canyon. **Owyhee:** Hot Spring. **Twin Falls:** Hansen, Hollister. ILLINOIS: **Macoupin:** Carlinville. INDIANA: **Porter:** Dune Acres. IOWA: **Polk:** Ankeny. **Woodbury:** Sioux City. KANSAS: **Barton:** Great Bend. **Douglas:** Lawrence (also 5 mi NW). **Grant:** —. **Kearny:** Lakin (also 9.5 mi S). **Marshall:** Blue Rapids. **Ness, Russell:** —. KENTUCKY (i): **Jefferson:** Louisville. **Marion:** Nerinx.

FIGURE 119. Geographic distribution of *Tachysphex apicalis* W. Fox

MICHIGAN: **Washtenaw:** Ann Arbor (Matthaei Botanical Garden). MISSOURI: **Boone:** Columbia. **St. Louis City:** St. Louis. MONTANA: **Dawson:** Glendive. **Garfield:** 5 mi W Jordan. **Powder River:** Broadus. **Rosebud:** Ashland. NEBRASKA: **Cherry:** Valentine. **Dawes:** Chadron. **Douglas:** Omaha. **Sioux:** Sawbelly Canyon, Toadstool Park. **Thomas:** Halsey, Nebraska National Forest (2.5 mi W Halsey), Thedford. NEVADA: **Churchill. Clark. Douglas:** Minden. **Elko:** Lamoille Canyon (Ruby Mts.). **Humboldt:** 5 mi E Golconda, Orovada, Soldier Meadows. **Lander:** 20 mi SW Austin. **Lincoln. Mineral:** 5 mi NW Schurz. **Nye:** 24 mi E Tonopah, 4 mi W Warm Springs. **Pershing:** 7 mi E Oreana. **Washoe. White Pine:** Baker. NEW JERSEY: **Gloucester:** Woodbury (i). NEW MEXICO: **Catron:** Pie Town. **Colfax:** 2 mi W Ute Park. **De Baca:** Sumner Lake State Park. **Dona Ana:** 12 mi N Las Cruces, Mesilla. **Eddy:** Carlsbad. **Guadalupe:** Santa Rosa. **Hidalgo:** 9 mi N Cotton City, Rodeo (also 18 mi N), Skeleton Canyon (Peloncillo Mts.). **Otero:** Alamogordo. **Quay:** Tucumcari. **San Juan:** 3 mi S Naschitt, Newcomb, 43 mi S Shiprock. **Sierra:** Percha Dam State Park. **Socorro:** La Joya (20 mi N Socorro). **Taos:** 17 mi NW Taos. NORTH CAROLINA: **Moore:** Southern Pines (se). **Onslow:** Onslow Beach (se). **Rowan:** Salisbury (i). **Wake:** Raleigh (i). NORTH DAKOTA: **Golden Valley:** Beach. **McHenry:** Towner. **Richland:** 13 mi W Walcott. OKLAHOMA: **Cimarron:** Black Mesa State Park. **Marshall:** 2 mi E Willis (Lake Texoma). OREGON: **Baker:** Robinette. **Deschutes:** 9 mi E Redmond. **Klamath:** Klamath Falls. **Wallowa:** 5 mi W Imnaha. PENNSYLVANIA: **Lehigh:** Lehigh Gap (i). SOUTH CAROLINA: **Greenville:** Greenville (i). **Union:** Santuc (i). TEXAS: **Bastrop:** 6 mi E Bastrop. **Bexar:** Fort Sam Houston. **Brewster:** Big Bend National Park (Castolon), Chisos Mts., 34 mi S Marathon. **Caldwell:** Luling, Maxwell. **Cameron:** Brownsville: **Comal:** New Braunfels. **Dallas:** Dallas. **Duval:** Benavides, 18 mi N San Diego. **Hidalgo:** Bentsen Rio Grande Valley State Park. **Hudspeth:** Fort Hancock, McNary, 5 mi N Sierra Blanca. **Jeff Davis:** 21 mi W Fort Davis, Limpia Canyon near Fort Davis. **Jim Wells:** Palito Blanco. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **Lee:** Fedor. **Pecos:** Sheffield. **Presidio:** 3 mi E Presidio. **Randall:** Palo Duro Canyon State Park. **Robertson:** Hearne. **San Patricio:** Corpus Christi, 5 and 10 mi NE Sinton. **Somervell:** Dinosaur Valley State Park. **Travis:** Austin. **Ward:** Monahans Sandhills State Park. **Williamson:** Taylor. **Young:** Newcastle. UTAH: **Box Elder:** Lucin. **Cache. Emery:** 9 air mi E Castle Dale, N Goblin Valley (Buckskin Spring, Wild Horse Creek), Highway 24 N Wayne County line. **Garfield:** Cass Creek Reserve, Mount Hillers (E slope), Shootaring Canyon. **Grand:** Arches National Monument. **Juan:** 12 mi S Eureka, 10 mi NE Leamington. **Millard:** Delta, Fillmore (also 12 mi NW), 10 mi W Patton. **Summit:** Wanship. **Tooele:** Delle. **Uintah:** SW Bonanza, 6 mi N Vernal, Watson. **Washington.** VIRGINIA: **Loudoun:** — WASHINGTON: **Benton:** Richland. **Franklin:** Hanford Reserve near Richland, Pasco. **Grant:** O'Sullivan Dam. **Okanogan:** Malott. **Whitman:** Wawawai. WISCONSIN: **Grant:** Rutledge. WYOMING: **Platte:** Wheatland. **Uinta:** Mountain View. **Weston:** New Castle.

MEXICO: **Baja California Norte:** El Consuelo. **Baja California Sur:** 30 mi ESE Bahia Tortugas, El Pescadero, 25 km SE Laguna Chapala, La Paz, Los Barriles, 4 mi WSW Miraflores, Playa Los Cerritos (11.2 mi S Todos Santos), 24 km W San Ignacio, 3 mi NE San Isidro. **Chihuahua:** 30 mi NW Ceballos, Chihuahua (also 35 mi NW), Samalayuca Dunes, Santa Clara Canyon (5 mi W Parrita). **Durango:** 5 mi W Durango. **Jalisco:** Guadalajara, Ixtlahuacán Del Rio. **Mexico:** Teotihuacán pyramids. **Morelos:** 3 mi N Alpuyeca. **Nayarit:** 22°20′N, 104°25′W. **Nuevo Leon:** Huasteca near Monterrey, S Montemorelos. **Oaxaca:** El Camaron (propodeum and wings as in Cuban specimens). **Puebla:** 3 mi NW Petlalcingo, 2 mi NW Tehuacan. **Sinaloa:** Chupaderos, 8 mi SE Elota, Topolobampo. **Sonora:** Alamos (also 10 mi SE), Bahía San Carlos, Ciudad Obregon, Cócorit, 5 mi W Santa Ana, 60 km NW Yecora. **Tamaulipas:** Ciudad Victoria, Matamoros. **Veracruz:** 5 mi SW Perote, Tinajas. **Zacatecas:** 15 mi E Sombrerete.

CUBA (Pulawski 1974*a*): **Oriente:** Ciudemar near Santiago de Cuba, Tortuguilla.

brullii Species Group

The *brullii* group (*bicolor* group of Pulawski 1971, 1974*a*) contains species in which the females have modified apical tarsomeres (males do not have group characters). The female's apical tarsomere is convex dorsally, its apicoventral margin is produced into a lobe or at least arcuate, and the venter is variously modified (covered with erect setae except glabrous basally or angulate basally in lateral view or densely spinose); the claws can be appressed to the venter of the apical tarsomere so that claw's apex reaches the tarsomere's base. In two South American species, *acutemarginatus* Strand and *pectinatus* Pulawski, the apical tarsomeres are weakly modified (the apicoventral margin is weakly arcuate), but I assigned them to the *brullii* group (Pulawski 1974*a*) because the setae of the propodeal dorsum are erect and slightly inclined posterad. In many species (including all North American), the female's pygidial plate is broadly rounded apically. In other groups the female's apical tarsomere is weakly convex dorsally, with the apicoventral margin straight or nearly so; the venter is evenly covered with setae that are mostly inclined (erect in *verticalis*), and a few spines are present in some species; the claws' movements are restricted so that their tips never reach the tarsomere's base. No character is known to distinguish the males of the *brullii* group from those of the *pompiliformis* group, but some features help in recognition. Setae of the propodeal dorsum (at least on its lateral and posterior parts) are erect or oriented posterad in most members of the *brullii* group. Exceptions to this are as follows. The anteriorly oriented setae form a narrow band from base to apex in the Australian *vardyi* Pulawski, and a broad band in *maya* and the Australian *politus* Pulawski and *vividus* Pulawski. All setae are inclined obliquely forward in *brevicornis* Pulawski (Australia) and the majority of species belonging to other groups. In *apricus* of the *pompiliformis* group, the basomedian setae are oriented obliquely anterad, but the lateral setae are oriented posterad toward the midline and join apicomesally (a condition found in most members of the *brullii* group).

Known prey in the *brullii* group are either tettigoniids or blattids. Tettigoniids are used by *belfragei, menkei, mundus,* and the Palearctic *brullii,* whereas blattids are prey of *alayoi, inconspicuus, iridipennis,* the Palearctic *blattivorus* Gussakovskij and *obscuripennis* (Schenck), the Australian *depressiventris* Turner, *fanuiensis* Cheesman from Oceania, and *nigerrimus* (F. Smith) from New Zealand. The shape of the female tarsus possibly is related to prey type, perhaps being an adaptation to a particular way of capturing or carrying prey. In the known tettigoniid hunters, the penultimate tarsomeres are about as wide as long, acutely emarginate dorsally, and roundly emarginate apicoventrally; the apical tarsomeres and claws are long, slender, and the apical tarsomeres are not angulate basoventrally in lateral view. Many other species of the *brullii* group have the same tarsi, and I expect them to be tettigoniid hunters as well. In all known blattid hunters, the penultimate tarsomeres are wider than long, obtusely angulate or rounded apically, and produced into a lobe apicoventrally; the apical tarsomeres and claws are short, stout, and the apical tarsomeres are angulate basoventrally in lateral view.

De Beaumont (1936) and also Menke (*in* Bohart and Menke 1976) placed the tettigoniid collectors and the roach hunters in two separate groups, the *brullii* group and the *obscuripennis* group, based on the shape of the female tarsi and nature of their prey. I have combined these two groups (Pulawski 1971, 1977*a*) because some species do not fit either of these categories and their prey is unknown. For example, in the Australian species *stimulator,* the penultimate tarsomere is wider than long, obtusely emarginate dorsally, and shallowly, roundly emarginate apicoventrally, and the apical tarsomere and the claws are long, but the tarsomere is slightly angulate basoventrally. In *verhoeffi* Pulawski (eastern Mediterranean), the penultimate tarsomere is slightly wider than long, roundly emarginate both ventrally and dorsally (shallowly so on venter), and the apical tarsomere and

tarsi are even longer and more slender than in *stimulator,* but the tarsomere is weakly angulate basoventrally. In the South American *acutemarginatus* Strand, the penultimate tarsomere is longer than wide, acutely emarginate dorsally, and almost straight apicoventrally, and the apical tarsomere and claws are short, stout, but not angulate basally. For convenience's sake, I recognize the *brullii* subgroup and the *obscuripennis* subgroup in this paper in spite of intermediates found in other zoogeographic regions.

The *brullii* group is cosmopolitan, but is dominant in the Australian Region (32 out of 40 known Australian species of *Tachysphex*).

brullii Subgroup

Vertex longer than wide (as long as wide in some males of *acanthophorus* and *aequalis*). Scutum and scutellum convex. Outer face of female foretibia with spines. Tarsomere IV longer than wide, with apical emargination acute (Fig. 121a), but roundly V-shaped in *menkei*; apicoventral margin concave mesally. Tarsomere V not angulate basoventrally in lateral view (Fig. 121b); claws slender, long (arolium attaining at most their midlength), more or less asymmetrical (one claw in each pair being slightly smaller than the other). Forebasitarsus with 9–14 rake spines in most species, but 7–9 in *armatus,* 5–9 in *acanthophorus,* and 5 in *cocopa.* Male foretarsus without rake, but outer apical spine of foretarsomere II may be as long as foretarsomere III in *menkei.*

Species of the *brullii* subgroup prey upon Tettigoniidae. They occur in all zoogeographic regions.

Tachysphex mundus W. Fox

(Figures 120–122)

Tachysphex exsectus W. Fox, 1894*a*:526, ♀, ♂. ! Lectotype: ♀, Montana: no specific locality (ANSP), designated by Cresson 1928:44. Synonymized with *mundus* by Pulawski *in* Krombein 1979:1632.—Dalla Torre 1897:679; Ashmead 1899: 250 (as *excatus*); G. Bohart 1951:951; Krombein 1967:393; Bohart and Menke 1976:273.—As *mundus exsectus*: Elliott and Kurczewski 1985:296.

Tachysphex mundus W. Fox, 1894*a*:531, ♀, ♂. ! Lectotype: ♀, Illinois: no specific locality (ANSP), designated by Cresson 1928:45.—Dalla Torre 1897:681; Ashmead 1899:250; H. Smith 1908:380; Stevens 1917:422; Mickel 1918:424; Robertson 1928:121, 128, 135; G. Bohart 1951:951; Krombein 1967:393; Bohart and Menke 1976:275; Kurczewski 1979:641 (life history).

Tachysphex johnsoni Rohwer, 1911:573, ♀. ! Holotype: ♀, Colorado: Washington Co.: Cope (USNM). **New synonym.** As synonym of *aequalis*: G. Bohart 1951: 950.

Diagnosis.—*Tachysphex mundus* can only be identified by a large suite of characters in combination. The head and thorax setae are straight in *mundus* (woolly in *menkei*), the scutal corner is rounded (Fig. 120c) (prominent in *maurus, robustior,* and *utina,* Fig. 125a, b), the scutal punctures are one diameter apart or less (more than one diameter apart in *menkei* and most *maurus*), the midscutal setae are oriented evenly posterad (oriented laterad in *acanthophorus, armatus,* and *cocopa*), the mesopleural punctures are fine or evanescent (large in *maya*), the propodeal dorsum is evenly microareolate (Fig. 120d, e) (rugose in *belfragei*), and the setae of the propodeal dorsum are oriented posterad except on a basomedian, triangular area where they are oriented anterad (Fig. 120d) (in *maya,* the setae are oriented anterad on a broad median zone that extends from the base to apex). In the female, the clypeal lip is not expanded (Fig. 120a) (expanded mesally in *belfragei* and *krombeiniellus,* Fig. 128a), tarsomere V has no basoventral spines (Fig. 121c) (present in *armatus*), or midventral spines (present in *armatus, cocopa,* and most *acanthophorus*). In the male, sterna III–VI have graduli (Fig. 121f) (a transverse sulcus in *acanthophorus, armatus,* and *cocopa*), sterna III–VI lack apical setal fasciae (present in *robustior*), and the tibiae are red (black in *aequalis, maurus, robustior,* and *utina*). The combination of red tibiae and an all black gaster is distinctive for many males of *mundus.* However, the gaster is partly red in many specimens, which may be confused with *krombeiniellus.* Unlike that species, the thoracic vestiture of *mundus* is silvery (and not golden), the vertex setae are inclined or erect (and not appressed), and the apical (broad) portion of the penis valve is not elongate. The distance between the clypeal lip corners of *mundus* is about equal the clypeal length (about 1.25 clypeal length in *aequalis*).

Females of *mundus* are very similar to *aequalis,* and their separation is complicated by exceptions. The gaster color of *mundus* is either all black or basally red. Black specimens are all *mundus,* but the bicolored ones may be either species. The closely punctate mesopleuron is diagnostic for *mundus,* but in some black specimens the punctures are two to three diameters apart. In *aequalis,* the gaster is bicolored (all red in some individuals), and the mesopleural punctures are two to five diameters apart (Fig. 123a, b). In addition, nearly all *mundus* lack spines on the lateroventral margin of hindtarsomere V, while in most *aequalis* one or two small spines are present. Also, *mundus* occurs east of the Rocky Mountains and *aequalis* west of the Rocky Mountains, but their ranges overlap in Colorado.

Description.—Scutum dull, not prominent posterolaterally (Fig. 120c), its punctures no more than one diameter apart. Mesopleuron markedly microsculptured, impunctate, or with shallow punctures that are less than one to slightly more than one diameter apart at middle, but up to two or three diameters apart in a female from Richmond, Texas (CAS) with all black gaster. Propodeal dorsum evenly microareolate (Fig. 120d, e); side conspicuously microsculptured, indistinctly microrugose in some specimens, rarely ridged posteriorly. Terga densely micropunctate.

Setae suberect to erect on vertex, appressed or nearly so on mesothorax and femora; integument easily visible. Scutal setae oriented posterad. Setae length (in MOD) 0.8 along hypostomal carina, 0.8–1.0 on vertex, 0.8–1.2 on propodeal dorsum.

Head and thorax black. Terga I–IV silvery fasciate apically. Wings weakly infumate to almost hyaline.

♀.—Labrum emarginate (Fig. 120b). Clypeus (Fig. 120a): bevel longer than basomedian area; lip not broadened, with or without median notch, with two lateral incisions on each side. Dorsal length of flagellomere I 1.3–1.9× apical width. Vertex punctures more than one diameter apart, at least mesally. Pygidial plate sparsely setose (Fig. 120f), broad or (few specimens) narrow. Tarsomere V of most specimens without spines on venter or margins (Fig. 121a–c), but one spine present on inner margin of left hindtarsomere in a female from Padre Island, Texas (CAS). Length 7.4–10.5 mm.

Femora black, tibiae black or with reddish zones, rarely red (some females of central United States form from Montana). A female from Moenkopi, Arizona, has all red hindfemur and hindtibia and largely red fore- and midtibia.

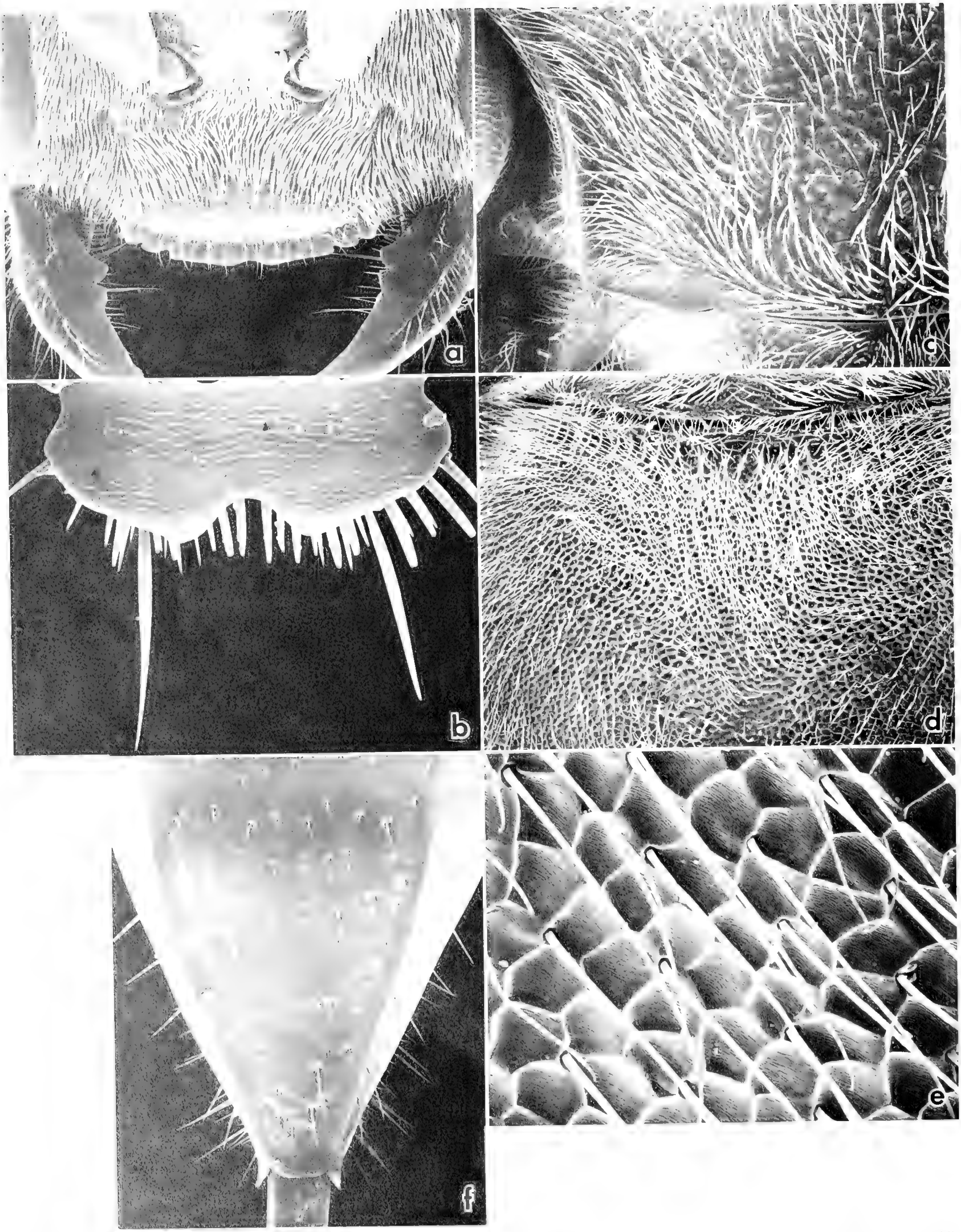

FIGURE 170. *Tachysphex mandus* W. Fox, female: a—clypeus, b—labrum, c—scutal hindcorner, d—propodeal dorsum (note anterad oriented setae in the middle and posterad oriented setae on the sides), e—sculpture of propodeal dorsum, f—pygidial plate.

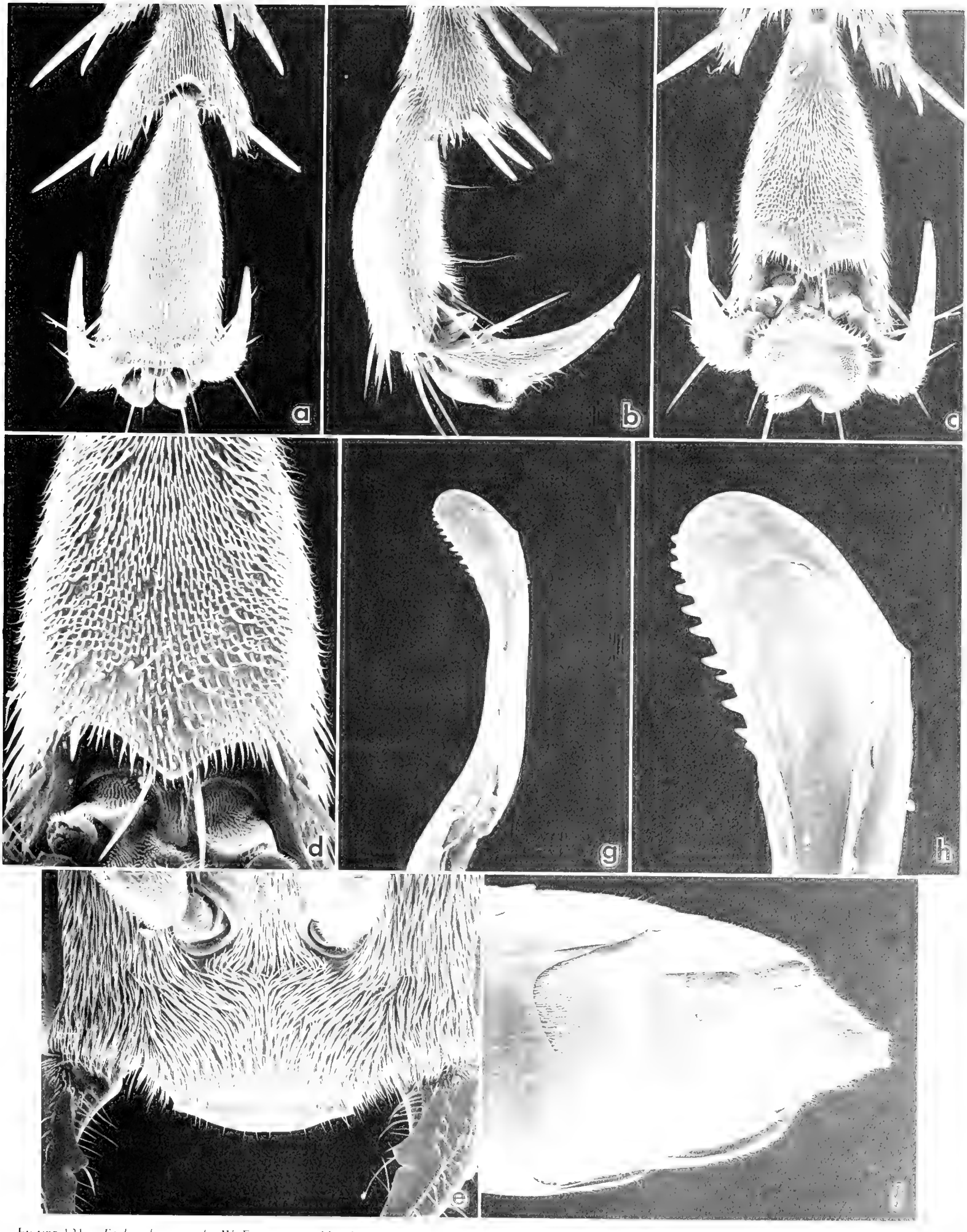

FIGURE 121. *Tachysphex mundus* W. Fox. a—apical hindtarsomere of female, dorsally; b—same, laterally; c—same, ventrally; d—same, higher magnification; e—male clypeus; f—gastral sterna of male; g—penis valve; h—penis valve, apical portion.

♂.—Clypeal bevel shorter than basomedian area or absent; lip arcuate or slightly concave on each side; distance between lip corners about equal to clypeal length (Fig. 121). Dorsal length of flagellomere I 1.1–1.4× apical width. Vertex punctures fine, about one diameter apart. Sterna pubescent throughout; sterna III–VI with graduli (Fig. 121f). Length 5.5–8.5 mm. Penis valve: Figure 121g, h.

Tibiae and tarsi red, frontal vestiture golden or (some specimens) silvery.

Geographic Variation.—*Tachysphex mundus* varies geographically in the color of the gaster as outlined below:

1) Gaster black in most individuals east of the Mississippi River (in all individuals from Florida and mid-Atlantic states), and also in many specimens west of Mississippi. This form can be called *mundus mundus* by those who accept trinominal nomenclature.

2) Gastral segments I to I–III are red in most individuals west of the Mississippi River and also in some specimens east of the Mississippi (including one from Raleigh, North Carolina). In addition, the mesopleuron usually has shallow, dense punctures. The name *mundus exsectus* (=*johnsoni*) is available for this form.

Individuals with an all black gaster, with reddish zones on terga I and II, and with red terga I and II, occur together in the following areas: Iowa: Ames and Sioux City; Kansas: Lawrence; Nebraska: Omaha and West Point; Wisconsin: Prescott, Rutledge, Olmsted Co.

Life History.—H. Smith (1908) observed this species on flowers of *Cassia* and *Euphorbia*, and Robertson (1928) on flowers of *Chamaecrista fasciculata* (Michx.) Greene (as *Cassia chamaecrista* (L.)), *Pycnanthemum flexuosum* (Walt.) B.S.P., and *Strophostyles helvola* (L.) Ell. The nesting behavior of *mundus* was studied by Kurczewski (1979). Females searching for a place to nest fly slowly over the ground in gravelly, sandy, or clayey areas. They land periodically, enter cracks and crevices in the soil, and open holes and burrows made by other insects, especially bees. They dig their own nests from the vertical burrows of bees or sphecids; in one case observed, two nests were excavated from a single burrow, but on opposite sides. A female began digging her nest with her mandibles and forelegs in the nest of the bee *Nomia heteropoda* (Say), 2 cm below the entrance. She dug in a lateral direction, nearly perpendicular to the bee shaft. Four times she interrupted her digging, left the tunnel headfirst, turned around, and reentered. Finally, she made several orientation flights and left the area. The nest of *mundus* is unicellular. The known prey consists mainly of nymphal tettigoniids: *Conocephalus* sp., *Orchelimum* sp., and a species that probably is *Odontosiphidium apertum* Morse. However, two cells in Kansas contained mixed prey: the tettigoniids *Conocephalus* sp. (eight nymphs) and *Orchelimum* sp. (five nymphs), and the gryllid *Oecanthus argentinus* Saussure (three nymphs). The prey are incompletely paralyzed, as demonstrated by movements of their antennae and mouthparts and breathing movements of the abdomen. They are transported to the nest in flight, dorsum up and head forward; their antennae are held with the wasp's mandibles; and their body is clutched with her legs. The wasp hovers above the entrance momentarily and then plunges inside (this description suggests that the nest is permanently open during the provisioning period). The prey are stored dorsum up or venter up, three to six per cell. No preference was observed in the choice of prey for egg deposition: it may be the heaviest or the lightest one, the one closest to the surface, or one laying on the cell floor. The egg is placed across the prey's body behind its forecoxa.

Geographic Distribution (Fig. 122).—North America east of the Rocky Mountains, north to Long Island, New York, Saskatchewan and southern Alberta, south to Florida and Tamaulipas, Mexico.

Material Examined.—203♀, 187♂ of form 1 (*mundus mundus*), and 97♀, 95♂ of form 2 (*mundus exsectus*)

Records (m: form 1; e: form 2).—CANADA: **Alberta** (e): Medicine Hat, 12 km S Orion, Picture Butte, Writing-on-Stone Provincial Park. **Saskatchewan** (e): Landing, 21 mi W Moose Jaw.

UNITED STATES: ALABAMA (m): **Baldwin:** Gulf Shores. ARIZONA (m): **Cochise:** Hereford. ARKANSAS: **Arkansas:** Arkansas River (m). **Hempstead:** Hope (e). COLORADO (e except Boulder): **Alamosa:** Great Sand Dunes. **Bent:** Hasty. **Boulder:** Boulder (partly b). **El Paso:** Colorado Springs. **Logan:** —. **Montrose:** Dolores Canyon. **Prowers:** Carlton. **Routt:** 7 mi E Hayden. **Washington:** Cope. **Weld:** Owl Creek (19 mi NE Nunn). DISTRICT OF COLUMBIA (m): Washington. FLORIDA (m): **Alachua:** Alachua, Gainesville, Monteoca (11 mi NW Gainesville). **Bradford:** —. **Brevard:** Cocoa. **De Soto:** Arcadia. **Flagler:** —. **Gadsden:** Quincy. **Gulf:** —. **Hardee:** Zolfo Springs. **Highlands:** Highlands Hammock State Park, Lake Annie, Lake Placid. **Leon:** Tall Timbers Research Station. **Levy:** Cedar Key. **Liberty:** Torreya State Park. **Orange:** Winter Park. **Polk:** —. **Putnam:** Crescent City, 2 mi NW Orange Springs, Palatka, Red Water Lake, Welaka. **Suwannee:** Suwannee River State Park. GEORGIA (m): **Charlton:** Billy's Island (Okefenokee Swamp). **De Kalb:** Stone Mountain. **Glynn:** Brunswick. **Macon:** Oglethorpe. **Mitchell:** DeWitt. **Richmond:** Augusta, Fort Gordon. **Tift:** Tifton. ILLINOIS: Chicago (e). **Macoupin:** Carlinville (m, e). **Mason:** Sand Ridge State Forest (m). IOWA: **Jackson:** Bellevue (m, e). **Story:** Ames (m, e). **Woodbury:** Sargeant Bluff (e), Sioux City (m, e). KANSAS (e if not indicated otherwise): **Dickinson, Reno:** —. **Douglas:** Lawrence (m, e). **Kiowa:** Belvidere. **Pottawatomie:** Blackjack Creek. **Scott:** —. MARYLAND (m): **Calvert:** Chesapeake Beach. **Prince Georges:** Beltsville, Patuxent Wildlife Research Center. MICHIGAN (m): **Gratiot:** —. **Livingston:** E. S. George Reserve. **Mecosta:** —. **St. Joseph:** Klinger Lake. MINNESOTA: **Hennepin:** Minneapolis (m). **Olmsted** (m, e): —. **Ramsey:** New Brighton (e). MISSISSIPPI (m): **Lafayette:** Oxford. MONTANA: —(e). NEBRASKA: **Cuming:** West Point (m, e). **Dawes:** Chadron (e). **Douglas:** Omaha (m, e). **Keith:** Ogallala (e). **Scotts Bluff:** Mitchell (e). **Sheridan:** Rushville (e). **Sioux:** Harrison (e), Monroe Canyon (e). Toadstool Park (m). **Thomas:** 2.5 mi W Halsey (m). NEW JERSEY (m): **Burlington:** Lebanon State Forest, Moorestown, Riverton. **Cape May:** —. **Union:** Westfield. NEW MEXICO: **Quay:** Tucumcari (e). **Roosevelt:** Oasis State Park (e). **Socorro:** La Joya (20 mi N Socorro) (e). NEW YORK: **Nassau:** Roslyn Heights (m). NORTH CAROLINA: **Brunswick:** Wilmington (m). **Cumberland:** Fort Bragg (m). **Moore:** Southern Pines (m). **Wake:** Raleigh (e). NORTH DAKOTA (e): **Burleigh:** Bismarck. **Golden Valley:** Beach. **Ransom:** 3 mi N McLeod, 7 mi SE Sheldon. OKLAHOMA: **Marshall:** Lake Texoma (2 mi E Willis) (m, e). SOUTH CAROLINA: **Aiken:** New Ellenton (m). SOUTH DAKOTA (e): **Butte:** Orman Dam. **Fall River:** Hot Springs. TENNESSEE: **Davidson:** Madison (m). TEXAS: **Anderson:** Salmon (m, e). **Aransas:** Aransas National Wildlife Refuge (m). **Atascosa:** Pleasonton (m, e). **Bastrop:** 6 mi E Bastrop (m). **Bexar:** Helotes (m), —(m, e). **Bosque:** Whitney Dam (m). **Brazos:** —(m). **Brewster:** 34 mi S Marathon (m), Rio Grande Village (m). **Caldwell:** Luling (e). **Comal:** New Braunfels (m). **Duval:** 18 mi N San Diego (m). **Fort Bend:** Richmond (m). **Hidalgo:** Edinburg (m), McAllen Botanical Garden (m). **Jim Wells:** Palito Blanco (m). **Kerr:** —(m). **Kenedy:** 3 mi S Sarita (e). **Kleberg:** Baffin Bay 20 mi SE Kingsville (m, e), Kingsville (m). **Lee:** Fedor (m, e). **Nueces:** Padre Island (e). **San Patrizio:** Aransas River 10 mi NE Sinton (e). **Travis:** Austin (m). **Victoria:** Victoria (e). **Ward:** S Grandfalls (m). **Williamson:** Taylor (m). VIRGINIA (m): **Arlington:** Arlington. **Fairfax:** Falls Church, Vienna. WISCONSIN: **Grant:** Rutledge (m, e), Wyalusing (m). **Pierce:** Prescott (m, e). **St. Croix:** Hudson (e). **Vernon:** Genoa (e).

MEXICO: **Tamaulipas:** Matamoros (m), Río Corona 18 mi N Ciudad Victoria (m)

Tachysphex aequalis W. Fox, revised status

(Figures 123, 124)

Larra rufitarsis Cameron, 1889:50, ♂, ! Holotype: ♂, Mexico: Sinaloa: Presidio near Mazatlán (BMNH). Nec Spinola, 1851. Synonymized with *aequalis* by Bohart and Menke 1976:272

FIGURE 122. Geographic distribution of *Tachysphex mundus* W. Fox.

Tachysphex aequalis W. Fox, 1894*a*:517, ♂. ! Lectotype: ♂, State of Washington: no specific locality (ANSP), designated by Cresson 1928:43. As synonym of *mundus*: Pulawski *in* Krombein 1979:1632.—Dalla Torre 1897:677; G. Bohart 1951:950; Bohart and Menke 1976:272.—As *Tachysphex mundus aequalis* Rust et al. 1985:46

Tachysphex opwanus Rohwer, 1911:574, ♂. ! Holotype: ♂, Colorado: Jefferson Co.: Golden (USNM). Synonymized with *aequalis* by G. Bohart 1951:950.

Tachysphex washingtoni Rohwer, 1917*a*:172, ♀. ! Holotype: ♀, Washington: Columbia River: Grand Coulee (USNM). Synonymized with *aequalis* by G. Bohart 1951:950

DIAGNOSIS.—*Tachysphex aequalis* closely resembles *mundus*, and both differ from the other species of the *brullii* subgroup by the characters given under *mundus* (page 169). Females of the two species differ as indicated under *mundus* (second paragraph of Diagnosis). Males of *aequalis* have black tibiae, and the distance between clypeal lip corners is equal to about 1.25 of the clypeal length (Fig. 123c) (in *mundus*, the tibiae are red, and the clypeal ratio is about 1.0).

DESCRIPTION.—Scutum not prominent posterolaterally, scutal punctures mostly less than one diameter apart (midscutal punctures up to two or three diameters apart mesally in some specimens). Mesopleural punctures well defined to evanescent, interspaces evenly microreticulate. Propodeal dorsum evenly microareolate; side evenly microreticulate, also punctate in some specimens. Terga densely micropunctate.

Setae suberect to erect on vertex, appressed or nearly so on mesothorax and femora; integument easily visible. Scutal setae oriented posterad. Setae length (in MOD) 0.8 on lower gena, 0.8–1.0 on vertex, 0.8–1.2 on propodeal dorsum.

Head and thorax black. Terga I–IV silvery fasciate apically. Wings weakly infumate to almost hyaline.

♀.—Labrum emarginate. Clypeal bevel longer than basomedian area; lip not broadened, with or without median notch, with two lateral incisions on each side. Dorsal length of flagellomere I 1.3–1.9 × apical width. Vertex punctures more than one diameter apart, at least mesally. Mesopleural punctures at middle two to five diameters apart (Fig. 123a, b), fine in most specimens, but rather coarse in certain individuals from Nevada and Utah. Pygidial plate with a few, sparse setae, usually broad, very rarely narrow. Tarsomere V of most specimens with one or two small spines on lateral margin. Length 7.5–10.0 mm.

Gastral segments I and II or I–III red, remainder black; all segments red in some females from Los Angeles, Orange, San Bernardino, and Santa Barbara counties, California, and in Baja California individuals. Femora and tibiae black in most specimens, but a female from Moenkopi, Arizona, has all red hindfemur and hindtibia and largely red fore- and midtibia.

♂.—Clypeal bevel shorter than basomedian area or absent; lip arcuate or slightly concave on each side; distance between lip corners equal to about 1.25 of clypeal length (Fig. 123c). Dorsal length of flagellomere I 1.1–1.4 × apical width. Vertex punctures fine, about one diameter apart. Mesopleural punctures subcontiguous to more than one diameter apart. Sterna pubescent throughout; sterna III–VI with graduli. Length 5.5–8.5 mm.

Gastral segments I and II or I–III red, remainder black (only tergum II and posterior half of sternum II red in some individuals). Femora black, tibiae all or largely black (but markedly red in one specimen from Wikieup, Arizona); tarsi red, dark basally. Frontal vestiture golden except silvery in smallest specimens.

DISCUSSION.—I previously (Pulawski *in* Krombein 1979) synonymized *aequalis* with *mundus*, considering it a geographic population of the latter. However, no intergradation between *aequalis* and *mundus* has been observed in the large numbers of specimens studied since and I now regard *aequalis* as a valid species.

Two females from Topock, Arizona (UCD), resemble *aequalis* in having the mesopleural punctures two to three diameters apart in the middle, but gaster is all black (except with small reddish zones on the sides of tergum I in one). I cannot determine whether these specimens are melanotic *aequalis* or members of some other species, e.g., *maurus*.

LIFE HISTORY.—Males of *aequalis* (CIS) were collected on flowers of *Foeniculum vulgare* Mill. at Artois, California, and of *Euphorbia* at Jacalitos Canyon, California. A female and a male from Logan, Utah (USU) were collected on flowers of *Daucus carota* L.

GEOGRAPHIC DISTRIBUTION (Fig. 124).—Southern British Columbia, United States west of the Rocky Mountains and also Black Hills National Forest area in eastern Wyoming, western Mexico south to Chiapas.

MATERIAL EXAMINED.—505♀, 799♂.

RECORDS.—CANADA: **British Columbia:** Mt. Robson, Vernon.

UNITED STATES: ARIZONA: **Cochise:** Ash Springs (Chiricahua Mts.), Portal (also 2 mi NE, 6 and 9 mi W). **Coconino:** 3 mi E Moenkopi. **Gila:** 3 mi SW Christmas. **Graham:** Roper Lake State Park. **Maricopa:** Wickenburg. **Mohave:** Topock, Wikieup. **Pima:** Continental, Sabino Canyon (Santa Catalina Mts.), Tucson. **Pinal:** 3 mi W Superior (Boyce Thompson Arboretum). **Santa Cruz:** Felton Springs, Madera Canyon (Santa Rita Mts.), Sycamore Canyon. **Yavapai:** Prescott. CALIFORNIA: **Alameda:** 2 mi NE Livermore, Sycamore Grove State Park. **Alpine:** Indian Creek Road (3 mi N Markleeville), Silver Creek, Woodfords. **Amador:** Plymouth. **Butte:** Oroville. **Calaveras:** Arnold, Mokell Hill. **Colusa:** Colusa. **Contra Costa. El Dorado:** 3.8 mi SW Somerset. **Fresno. Glenn:** Artois, 2 mi N Glenn, Willows. **Humboldt:** Garberville. **Inyo. Kern:** Antelope Canyon near Tehachapi, Frazier Park, Mill Potrero. **Lake:** Bartlett Spring. **Lassen:** Hallelujah Junction. **Los Angeles. Marin. Mariposa:** Mariposa. **Mendocino:** Hendy Groves State Park, 2 mi S Hopland, Navarro. **Modoc:** Cedar Pass, Davis Creek, Lake City. **Mono. Monterey. Napa:** Bitter Creek (Lake Lommel, vicinity Calistoga). **Nevada:** Nevada City. **Orange:** Corona del Mar, Peters Canyon. **Placer:** Auburn, Emigrant Gap, Weimar. **Plumas:** Lake Almanor, 6 mi E Spring Garden. **Riverside. Sacramento. San Benito:** Idria (Gem Mine). **San Bernardino:** Cajon, Mill Creek, San Bernardino Mts. (Coon Creek, Mountain Home Creek), S Fork of Santa Ana River, Wildwood Canyon (5 mi E Calimesa), 3 mi S Yucaipa. **San Diego. San Joaquin:** Tracy. **San Luis Obispo:** Dune Lakes (3 mi S Oceano), Montana de Oro State Park (3 mi SW Los Osos), Morro Bay. **San Mateo:** Menlo Park, Redwood City. **Santa Barbara:** including Santa Cruz Island. **Santa Clara:** Alum Rock Park, San Jose, Stanford University. **Santa Cruz:** Felton Springs (also 25 mi N), Lockhart Gulch (5 mi E Mt. Hermon), Santa Cruz Mts. **Shasta. Sierra:** Sierraville. **Siskiyou:** Etna, McBride Springs (3 mi NNE Mount Shasta town), Mount Shasta town. **Solano:** Benicia, Rio Vista, Vallejo. **Sonoma:** Healdsburg, Laguna de Santa Rosa, Petaluma. **Stanislaus:** Del Puerto Canyon, La Grange. **Trinity:** Junction City. **Tulare:** Lemon Cove, Three Rivers, Woodlake. **Tuolumne:** Strawberry. **Ventura. Yolo. Yuba:** 12 mi S Marysville. COLORADO: **Boulder:** Boulder. **Garfield:** Rifle. **Jefferson:** Golden. **Larimer:** Fort Collins, Glacier View Meadow (15 mi W Livermore). **Mesa:** Mack. **Montezuma:** 13 mi W Arriola. **Montrose:** Dolores Canyon. IDAHO: **Ada:** 12 mi NE Regina. **Blaine:** 3 mi W Carey. **Butte:** Craters of the Moon National Monument. **Canyon:** Notus. **Cassia:** Emery Canyon (12 mi SE Oakley), Sublette. **Elmore:** Dixie. **Franklin:** 3 mi NW Preston. **Gooding:** 1 mi NE Gooding. **Idaho:** 8 mi N Riggins. **Kootenai:** Coeur d'Alene. **Lemhi:** 3 mi N North Fork. **Lincoln:** Richfield. **Nez Perce:** Lewiston. **Oneida:** 5 mi NW Holbrook, Salyer Cow Camp, Twin Springs. **Owyhee:** 4 mi SW Bruneau, Bruneau River 20 mi N Three Creek, Hot Springs, 2 mi SW Murphy. **Payette:** 32 mi S Indian Valley. **Twin Falls:** Rock Creek Canyon (Deer Creek). MONTANA: **Sanders:** Dixon. NEVADA: **Clark:** Charleston Mts. (Willow Creek Camp). **Douglas:** 3 mi S Genoa, Minden. **Elko. Eureka:** Beowawe, 1 mi W Emigrant Pass. **Humboldt:** Orovada, Paradise Valley. **Lander:** Austin, Kingston Canyon. **Lyon:** Fernley, Smith, 5 mi N Sweetwater.

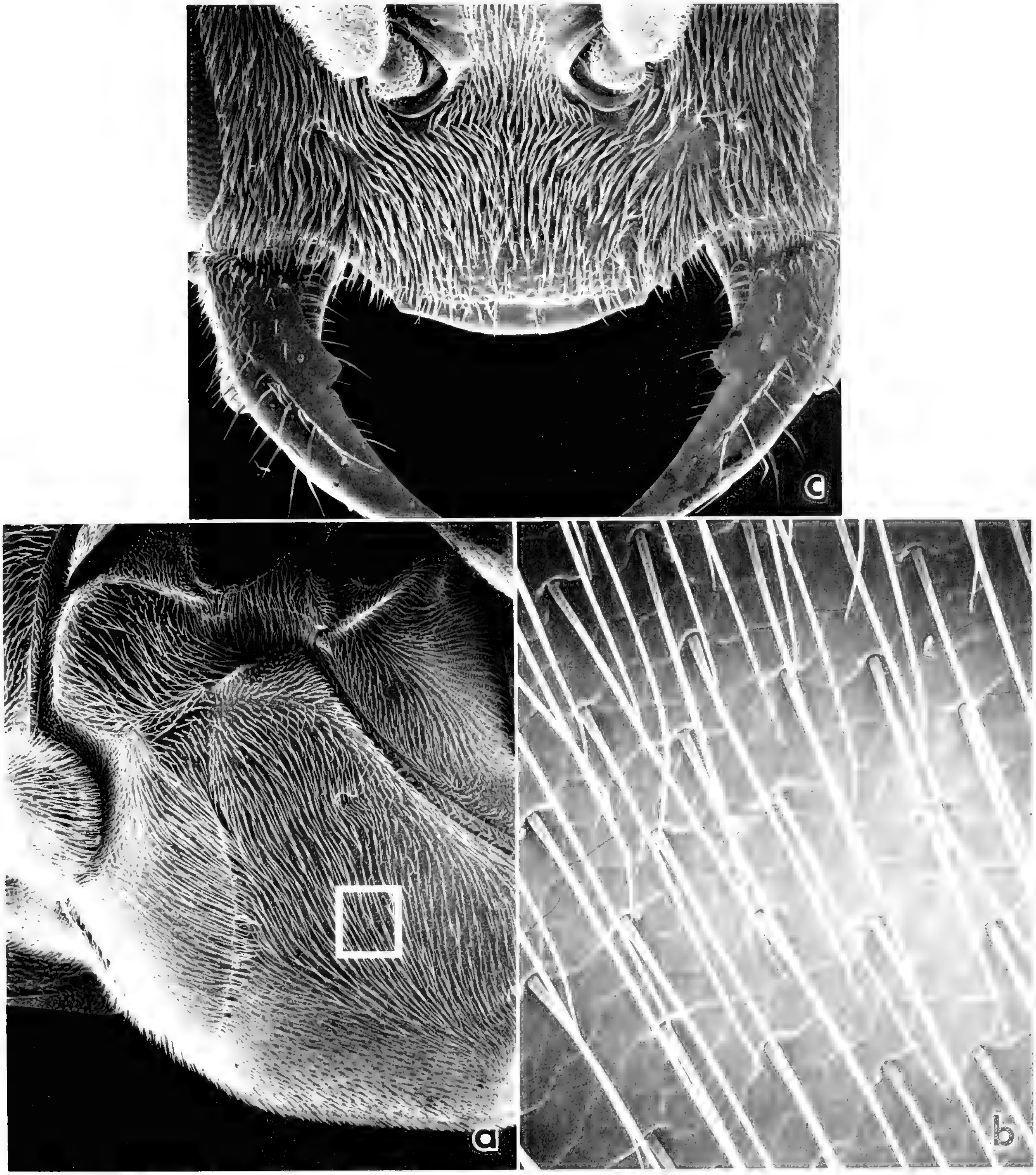

FIGURE 123. *Tachysphex aequalis* W. Fox: a—female mesopleuron (box: area shown in b); b—area shown in box of a; c—male clypeus

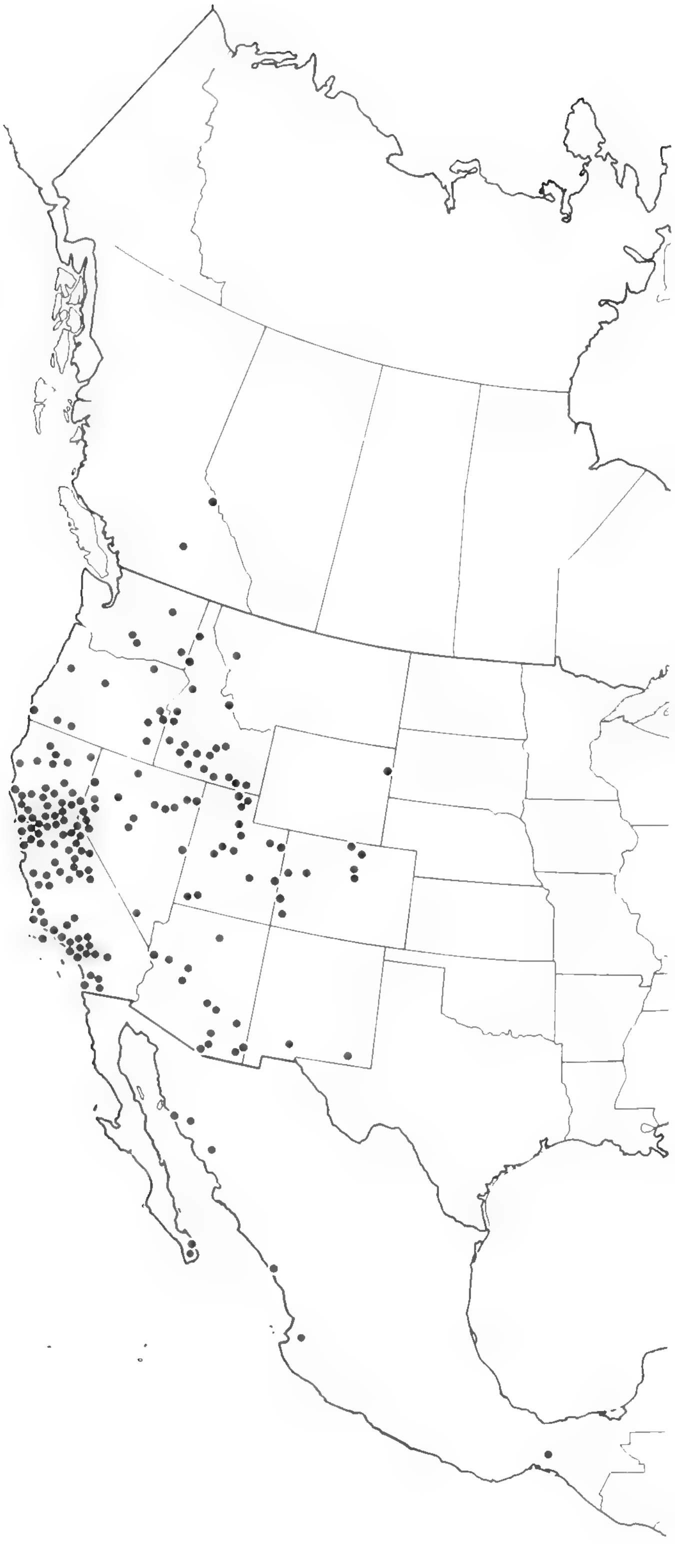

FIGURE 124 Geographic distribution of *Tachysphex aequalis* W. Fox

Ormsby: —. **Pershing:** 7 mi E Oreana. **Washoe. White Pine:** Baker. NEW MEXICO: **Dona Ana:** Las Cruces, Leasburg Dam State Park. **Eddy:** Carlsbad. OREGON: **Benton:** Corvallis. **Curry:** Gold Beach. **Deschutes:** Smith Rock State Park. **Jackson:** Brownsboro, Medford. **Klamath:** 10 mi E Dairy, 4 mi N Klamath Falls. **Malheur:** 6 mi E Burns Junction, 4 and 8 mi E Juntura, 11 mi W Ontario, 18 mi NW Vale. **Umatilla:** Pendleton. UTAH: **Box Elder. Cache. Duchesne:** Myton. **Emery:** N Goblin Valley (Buckskin Spring, Wild Horse Creek), NE Goblin Valley (3 and 4 air mi N Gilson Butte, 2 mi E Gilson Butte). **Grand:** Castleton. **Millard:** Delta, Lynndyl. **Rich:** Allen Canyon. **Salt Lake:** Salt Lake City. **Sanpete:** Moroni. **Uintah:** 17 mi S Bonanza, Gusher. **Utah:** Hobble Creek Canyon, Provo. **Washington.** WASHINGTON: **Grant:** Grand Coulee. **Whitman:** Wawawai. **Yakima:** Buena, Yakima. WYOMING: **Weston:** Newcastle.

MEXICO: **Baja California Sur:** Los Barrilles, 4 mi WSW Miraflores. **Chiapas:** 28 mi W Cintalapa. **Jalisco:** Plan de Barrancas. **Sinaloa:** Presidio near Mazatlán. **Sonora:** Aduana, Cócorit, 6 km NNW San Carlos.

Tachysphex robustior Williams, revised status

(Figures 125, 126)

Tachysphex robustior Williams, 1914:164, ♂, ! Holotype ♂: Kansas: Grant Co.: no specific locality (KU).—G. Bohart 1951:952; LaBerge 1956:527; Arnaud 1970:33; Bohart and Menke 1976:276; Pulawski *in* Krombein 1979:1632 (as synonym of *mundus*).

Tachysphex crenuloides Williams, 1914:168, ♀, ! Holotype ♀: Kansas: Morton Co.: no specific locality (KU). Synonymized with *robustior* by G. Bohart 1951:952.—LaBerge 1956:527; Arnaud 1970:32

DIAGNOSIS.—Females of *robustior* can be recognized by a prominent scutal hindcorner (Fig. 125a) combined with black tibiae and a basally red gaster. Possibly some females are all black (as are some males), and such individuals could be confused with *maurus* and *utina*. However, the scutal punctures of *robustior* are less than one diameter apart, with dull interspaces, and the axilla is evenly convex. In *maurus*, midscutal punctures are more than one diameter apart or slightly less, and the interspaces are shiny. In *utina*, the axilla is steplike laterally. The male of *robustior* has a distinctive sternal feature: the setae of sterna III–V exceed the sternal hindmargin and form regular although small fasciae (Fig. 125c). Also, the combination of a basally red gaster and the prominent scutal hindcorner is distinctive for most specimens. Like *maurus* and *utina*, the frontal vestiture of *robustior* is silvery, but golden in most *aequalis* and most *mundus*.

DESCRIPTION.—Scutum shiny, prominent posterolaterally (Fig. 125a, b), but weakly so in some females; scutal punctures less than one diameter apart. Mesopleuron microsculptured and punctate, punctures of most specimens less than one diameter apart, but up to two diameters apart in a female from Big Bend National Park, Texas (UCD). Propodeal dorsum evenly microareolate; side microsculptured, with inconspicuous punctures.

Setae appressed to suberect on vertex, appressed or nearly so on scutum and femora, subappressed to suberect on mesopleuron. Scutal setae oriented posterad. Setae length (in MOD): up to 1.3 adjacent to hypostomal carina, about 0.7 on vertex, 1.0–1.3 on propodeal dorsum.

Head, thorax, and legs black, tarsal apex reddish. Frontal vestiture silvery.

♀.—Labrum emarginate. Clypeal bevel about as long as basomedian area; lip not broadened, with or without median emargination, with two lateral incisions on each side. Dorsal length of flagellomere I 1.8–2.2 × apical width. Most vertex punctures less than one diameter apart, but some punctures up to one or two diameters apart. Pygidial plate with a few, sparse setae. Tarsomere V without spines on venter or lateral margins. Length 6–8 mm.

Gaster all red, or segments IV–VI or III–VI black (females from Port Isabel, Matamoros, and some from Fedor, Texas), or gaster predominantly black, with translucent apical depression and narrow reddish zones (a female from Jiménez area, Mexico).

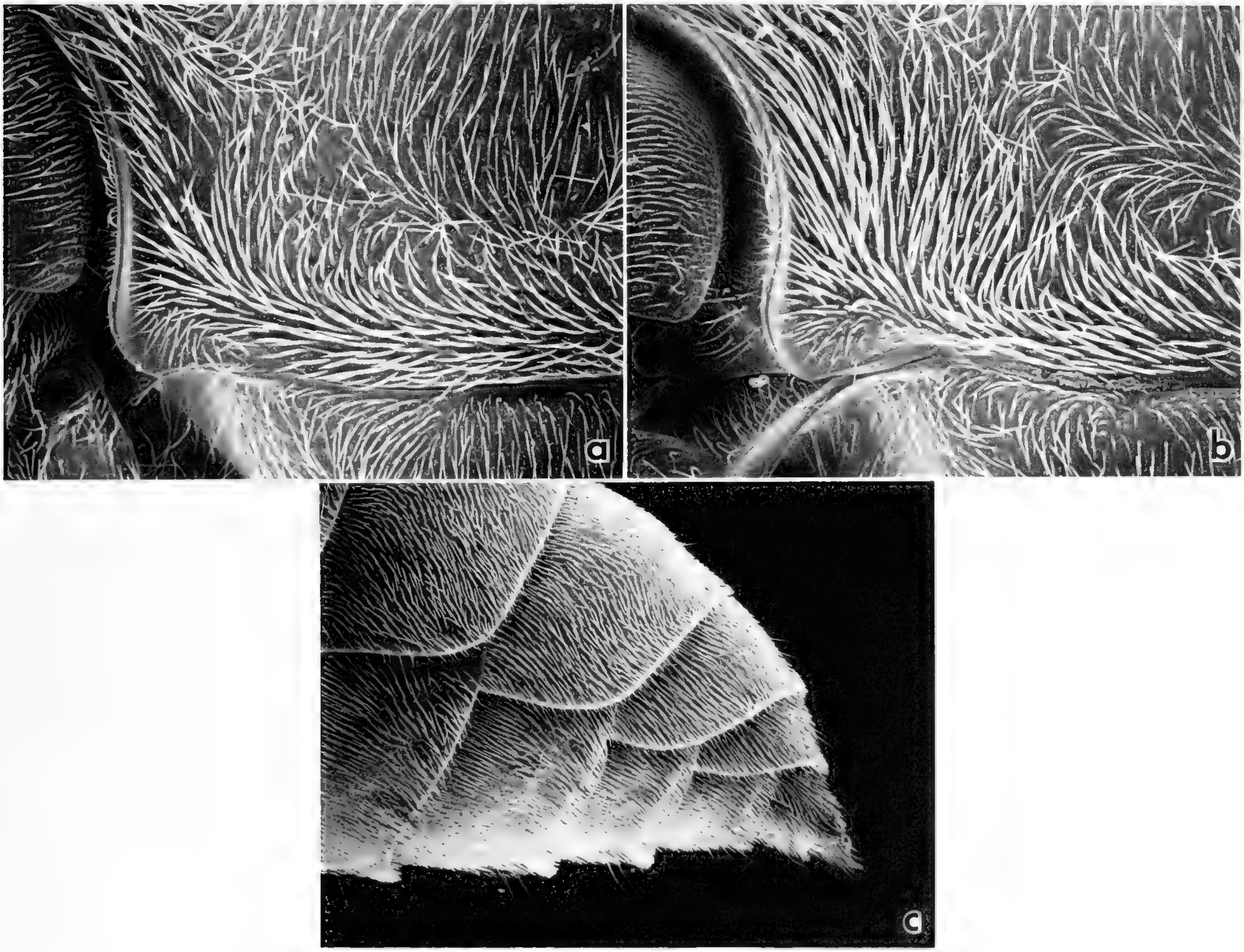

FIGURE 125. *Tachysphex robustior* Williams: a—scutal hindcorner of female; b—scutal hindcorner of male; c—gastral apex of male.

♂.—Clypeal bevel shorter than basomedian area; lip arcuate, distance between its corners about equal to clypeal length. Dorsal length of flagellomere I about 1.2× apical width. Vertex punctures less than one diameter apart in some individuals, one to two diameters apart in others. Sterna pubescent throughout, setae of sterna III–V forming apical fasciae that extent beyond sternal hindmargin (Fig. 125c). Sterna III–VI with graduli. Length 5.5–7.0 mm.

Gastral segments I and II or I–III red in most specimens, but gaster all black in a male from San Carlos, Sonora (UCD).

DISCUSSION.—I previously synonymized (Pulawski *in* Krombein 1979) *robustior* with *mundus* because only chromatic differences between the two were known to me. These differences seemed no more significant than those between the two color phases of *mundus* (*mundus mundus* and *mundus exsectus*). However, the distinctive sternal fasciae in the male of *robustior* demonstrate that it is a valid species. The structure is unique, and no intermediates have been observed. The prominent scutal hindcorner is also significant.

GEOGRAPHIC DISTRIBUTION (Fig. 126).—Arizona to southeastern Texas, north to Colorado and Kansas, south to Sonora, Chihuahua, and Tamaulipas states in Mexico.

MATERIAL EXAMINED.—51♀, 54♂ (CAS, CNC, CSDA, CSU, FSCA, MCZ, NYSU, TAI, UAT, UCD, USNM, USU)

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** Hereford, Portal. **Pima:** Continental, Saguaro National Monument, Tucson. COLORADO. **Bent:** 2 mi S Hasty. KANSAS: **Grant, Morton, Reno:** —. **Kearny:** Lakin. NEW MEXICO: **Luna:** Columbus. TEXAS: **Brewster:** Big Bend National Park (Nine Point Draw, Santa Elena Canyon). **Cameron:** Port Isabel. **Culberson:** Pine Springs. **Hudspeth:** Salt Flat. **Kleberg:** Baffin Bay 6 mi E Riviera (=20 mi SE Kingsville). **Lee:** Fedor **Maverick:** Quemado. **San Patricio:** Welder Wildlife Refuge (7 mi NE Sinton)

MEXICO: **Chihuahua:** 18 mi W Jiménez. **Coahuila:** 19 km W Cuatrociénegas **Sonora:** San Carlos. **Tamaulipas:** Matamoros (also 30 mi SE), Playa Altamira Rio Corona 18 mi N Ciudad Victoria

Tachysphex maurus Rohwer

(Figure 127)

Tachysphex maurus Rohwer, 1911:575, ♀, ♂. ! Lectotype: ♂, Texas: Lee Co.: Fedor (USNM), present designation.—G. Bohart 1951:951; Bohart and Menke 1976 274; Krombein 1979:1632

DIAGNOSIS.—*Tachysphex maurus* is an all black species with a prominent scutal hindcorner (see Fig. 125a, b), a combination also found in *utina* and some *robustior*. However, the midscutal punctures of *maurus* average more than one diameter apart (slightly less than one diameter apart in some males), and the

FIGURE 126. Geographic distribution of *Tachysphex robustior* Williams.

interspaces are shiny. In the other two species, the midscutal punctures are less than one diameter apart, and the interspaces are dull. Unlike *utina*, the axilla of *maurus* is not steplike laterally. Unlike *robustior*, male sterna of *maurus* are not fasciate apically. Many females of *mundus* are also all black, but they have a rounded scutal hindcorner (Fig. 120c), and their midscutal punctures are less than one diameter apart.

DESCRIPTION.—Scutum shiny, prominent posterolaterally (weakly so in female); midscutal punctures averaging more than one diameter apart, except slightly less than one diameter apart in some males. Mesopleuron weakly microsculptured, shiny, with well-defined punctures that are one to two diameters apart at middle. Propodeal dorsum evenly microreticulate or (some males) weakly rugose; side punctate or (some males) rugose.

Setae suberect to erect on vertex, appressed or nearly so on mesothorax and femora. Scutal setae oriented posterad. Setae length (in MOD): 0.8 along hypostomal carina, 0.8–1.0 on vertex, 0.8–1.2 on propodeal dorsum.

Head, thorax, and gaster black; legs black, tarsal apex brown, tibiae of some males partly brown. Frontal vestiture silvery.

♀.—Labrum emarginate. Clypeal bevel longer than basomedian area; lip not broadened, with or without mesal notch, with two lateral incisions on each side. Dorsal length of flagellomere I 1.4–1.8× apical width. Punctures more than one diameter apart on vertex (at least mesially). Pygidial plate broad, with few, sparse setae. Tarsomeres V without spines on venter or lateral margins. Length 7–11 mm.

♂.—Clypeal bevel shorter than basomedian area or absent; lip arcuate, distance between corners varying from about one (most specimens) to about 1.25 of clypeal length. Dorsal length of flagellomere I 1.1–1.3× apical width. Vertex punctures fine, about one diameter apart. Sterna pubescent throughout, but without setal fasciae at hindmargins; sterna III–VI with graduli. Length 4.8–8.0 mm. Penis valve as in *mundus*.

GEOGRAPHIC DISTRIBUTION (Fig. 127).—Southern Oklahoma, Texas, Arizona, Mexico, south to Costa Rica.

MATERIAL EXAMINED.—49♀, 86♂ (AMNH, CAS, CIS, CSDA, CU, FSCA, KU, NYSU, MCZ, TAI, UAT, UCD, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** 5 and 13 mi SE Apache (also 11 mi S), 28 mi N Douglas, Miller Canyon (Huachuca Mts.), Portal. **Graham:** Roper Lake State Park (7 mi S Safford). **Pima:** Molino Basin (Santa Catalina Mts.), Tucson. **Pinal:** Coolidge. **Santa Cruz:** Nogales (also 5 mi E), Sycamore Canyon (Ruby Road), Walker Canyon (6 mi NW Nogales). NEW MEXICO: **Dona Ana:** Leasburg Dam State Park. OKLAHOMA: **Marshall:** Lake Texoma (2 mi E Willis). TEXAS: **Atascosa:** Pleasanton. **Bastrop:** 6 mi E Bastrop. **Bosque:** —. **Caldwell:** Luling. **Dallas:** Dallas. **Duval:** 18 mi N San Diego. **Hidalgo:** Bentsen Rio Grande Valley State Park. **Kimble:** Junction. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **Lee:** Fedor. **Uvalde:** Nueces River 12 mi S Uvalde, 30 mi N Uvalde.

MEXICO: **Chihuahua:** 10 mi N Chihuahua. **Colima:** 23 mi N Manzanillo. **Guerrero:** Acapulco. **Jalisco:** Chamela. **Morelos:** 5 mi E Cuernavaca. **Nayarit:** Jesús María. **Oaxaca:** 23 mi S Matías Romero. **Sinaloa:** 6 mi NW Choix, 34 mi N Los Mochis, 2.5 and 5 mi N Mazatlán. **Sonora:** Alamos (also 10 mi SE), Magdalena, 28 mi S Navajoa, Nogales, San Carlos, E of Yaqui River (35 air km WSW Sahuaripa). **Zacatecas:** San Juan Capistrano (22°38′N, 104°05′W).

CENTRAL AMERICA: COSTA RICA, Junquillal Beach (Guanacaste Prov.).

Tachysphex utina sp. n.

(Figure 127)

DERIVATION OF NAME.—Utina is a Florida Indian name that probably refers to the chief and means powerful; noun in apposition.

DIAGNOSIS.—*Tachysphex utina* has an all black body and a prominent scutal hindcorner (see Fig. 125a, b), a combination also found in *maurus* and some *robustior*. In *utina*, the axilla is steplike (only weakly so in the female), the scutal punctures are less than one diameter apart, with dull interspaces, and male sterna are not fasciate apically. In the other two species, the axilla is gradually sloping laterad. In addition, scutal punctures

FIGURE 127. Geographic distribution of *Tachysphex maurus* Rohwer and *utina* sp. n.

of most *maurus* average more than one diameter apart (slightly less than one diameter in some males), and the interspaces are shiny; and in *robustior*, male sterna III–V are fasciate apically (Fig. 125c). Geographic distribution also aids identification: *utina* occurs along the Atlantic Coast between New Jersey and Florida, while *maurus* and *robustior* are found west of the Mississippi River.

Description.—Vertex punctures one to two diameters apart. Scutum weakly shiny, prominent posterolaterally (weakly so in female). Axilla peculiar, steplike, overhanging sloping (lateral) part. Mesopleuron microsculptured, with minute punctures that are more than one diameter apart. Propodeal dorsum evenly microareolate; side microsculptured, with inconspicuous punctures.

Setae suberect on vertex, appressed on scutum and femora; suberect on mesopleuron. Scutal setae oriented posterad. Setae length (in MOD): 0.7–1.0 adjacent to hypostomal carina, about 0.7 on vertex, 1.0–1.3 on propodeal dorsum.

Head, thorax, gaster, and legs black. Frontal vestiture silvery. Wings weakly infumate.

♀.—Labrum emarginate. Clypeal bevel about as long as basomedian area; lip not broadened, mesally entire or emarginate, with two lateral incisions on each side. Dorsal length of flagellomere I 1.6–1.7× apical width. Midscutal punctures averaging less than one diameter apart. Axilla sloping more steeply laterad than in *mundus*. Pygidial plate with few, sparse setae. Tarsomere V without spines on venter or lateral margins. Length 7–8 mm.

♂.—Clypeal bevel absent; lip arcuate, distance between its corners about equal clypeal length. Dorsal length of flagellomere I about 1.3–1.4× apical width. Midscutal punctures averaging about one diameter apart. Axilla peculiar, sloping almost vertically laterad. Sterna densely pubescent, but without setal fasciae apically. Sterna III–VI with graduli. Length 6.0–6.3 mm.

Discussion.—*Tachysphex utina* and *maurus* are very similar morphologically. They are allopatric and thus they may be geographic forms of one species. However, intermediates have not been seen.

Geographic Distribution (Fig. 127).—New Jersey to Florida.

Collecting Period.—14 April (Florida) through 31 July (New Jersey).

Material Examined.—Holotype: ♀, Florida: Putnam: Welaka, 1–4 May 1955, HEE and M. A. Evans (USNM).

Paratypes (14♀, 9♂). UNITED STATES: FLORIDA: **Alachua:** Gainesville, 17 May 1976, W. H. Pierce (1♀, UCD), 14–19 May 1976 (Austin Carey Memorial Forest), G. B. Fairchild (1♂, FSCA), 16–20 July 1975, EEG (1♀, FSCA). **Highlands:** Archbold Biological Station, 14 Apr 1968, J. G. and B. L. Rozen (1♀, AMNH), 5 and 31 May 1981, L. L. Lampert (2♀, CAS, FSCA). **Levy:** Cedar Key, 18 May 1970, D. L. Bailey (2♂, CAS, USNM). **Okaloosa:** 4.5 mi N Holt, 17 June 1978, LAS (1♀, 1♂, FSCA). **Putnam:** Georgetown, 30 Apr 1955, HEE and M. A. Evans (1♀, head missing, MCZ), Welaka, same data as holotype (1♂, MCZ; 1♀, 1♂, USNM). **Sarasota:** ocean beach, 3 June 1954, H. V. Weems (1♀, FSCA). GEORGIA: **Ware:** 8.2 mi N Waycross, 18 July 1969, N. Burdick (1♂, CAS, 1♀, 1♂ NYSU). NEW JERSEY. **Monmouth:** Little Silver, 31 July 1979, A. Hook (2♀, CAS, CSU). SOUTH CAROLINA: **Aiken:** Aiken, 23 June 1957, W. R. M. Mason (1♀, CAS; 1♀, 1♂, CNC).

Tachysphex belfragei (Cresson)

(Figures 128–130)

Larra Belfragei Cresson, 1872:215, ♀ (incorrect original spelling). ! Holotype: ♀, Texas: Bosque Co.: no specific locality (USNM).—Patton 1881:389; Kohl 1885: 242; Cresson 1916:95.—In *Tachysphex*: W. Fox 1894*a*:509; Dalla Torre 1897: 678 (as *belfragii*); Ashmead 1899:250; H. Smith 1908:381; Williams 1914:164; Mickel 1918:421; Robertson 1928:121, 128, 163, 199, 203; G. Bohart 1951: 950; Krombein 1958*c*:188, 1967:392; Bohart and Menke 1976:272; Krombein 1979:1632.

Tachytes minimus W. Fox, 1892:248, ♂. ! Lectotype: ♂, Texas: no specific locality (ANSP), designated by Cresson 1928:45. Synonymized by R. Bohart *in* Bohart and Menke 1976:272.—In *Tachysphex*: W. Fox 1894*a*:532; Dalla Torre 1897: 681; Ashmead 1899:250; J. Smith 1900:518; H. Smith 1908:381; J. Smith 1910: 683; Williams 1914:173; Mickel 1918:421; Brimley 1938:443; Krombein 1939: 139; G. Bohart 1951:951; Krombein and Evans 1954:232, 1955:231; Kurczewski 1971:114 (in key).

Diagnosis.—The coarsely sculptured propodeal dorsum (Fig. 128b), or finely rugose in many males, separates *belfragei* from all other New World species of the *brullii* subgroup. The female also differs from other species except *krombeiniellus* in having a mesally expanded clypeal lip (Fig. 128a) and an apically biemarginate basal platform of sternum II (Fig. 128c).

Description.—Mesothoracic punctures subcontiguous, somewhat ill defined on mesopleuron (where the integument is dull). Scutum rounded posterolaterally. Propodeal dorsum coarsely, irregularly rugose (Fig. 128b), but finely rugose in many males; side ridged. Terga densely micropunctate.

Setae appressed on vertex, mesothorax, and femora; underlying integument easily visible. Scutal setae oriented posterad.

Femora black (except red apically), tibiae and tarsi red. Terga I–IV (I–V in some males) silvery fasciate apically. Wings yellowish.

♀.—Labrum emarginate mesally. Clypeal bevel shorter to longer than basomedian area; lip broadened mesally, emarginate mesally in nearly all specimens, with two lateral incisions on each side (Fig. 128a). Dorsal length of flagellomere I 1.6–1.9× apical width. Vertex punctures less than one diameter apart, in many specimens more than one diameter apart near orbits. Basal platform of sternum II with biemarginate apical margin. Pygidial plate narrow, densely setose apically (Fig. 128d). Tarsomere V without spines on venter and lateral margins. Length 7.5–11.0 mm.

Setae length about 1.0–1.2 MOD along hypostomal carina and on propodeal dorsum.

Gastral segments I and II or I–III red, remainder black.

♂.—Clypeal bevel convex, shiny, shorter than basomedian area; lip broadly arcuate, corners indistinct and obtuse or prominent and rectangular, separated by a distance that is about equal to clypeal length. Dorsal length of flagellomere I 1.2–1.6× apical width. Vertex with fine, well-defined punctures that are less than one diameter apart. Sterna densely punctate and pubescent, but without setal fasciae on hindmargins; sterna III–VI with graduli. Length 6.5–7.5 mm. Penis valve: Figure 129.

Setae length 0.6–0.8 MOD along hypostomal carina and on propodeal dorsum.

Gaster black or segments I and II partly red. Frontal vestiture silvery or with golden tinge.

Life History.—H. Smith (1908) observed *belfragei* on flowers of *Euphorbia*, Mickel (1917) on flowers of *Chamaecrista fasciculata* (Michx.) Greene, and Robertson (1928) on flowers of *Chamaecrista fasciculata* (Michx.) Greene (as *Cassia chamaecristata* (L.)), *Ceanothus americanus* L., *Cicuta maculata* L., *Eryngium yuccifolium* Michx., *Oxypolis rigidior* (L.) C. and R., and *Pycnanthemum flexuosum* (Walt.) B.S.P. The species preys upon nymphs of *Conocephalus* sp., a tettigoniid (Krombein 1967). Kurczewski (1979) observed a female transporting a nymph of *Conocephalus* on the ground. She held the prey's

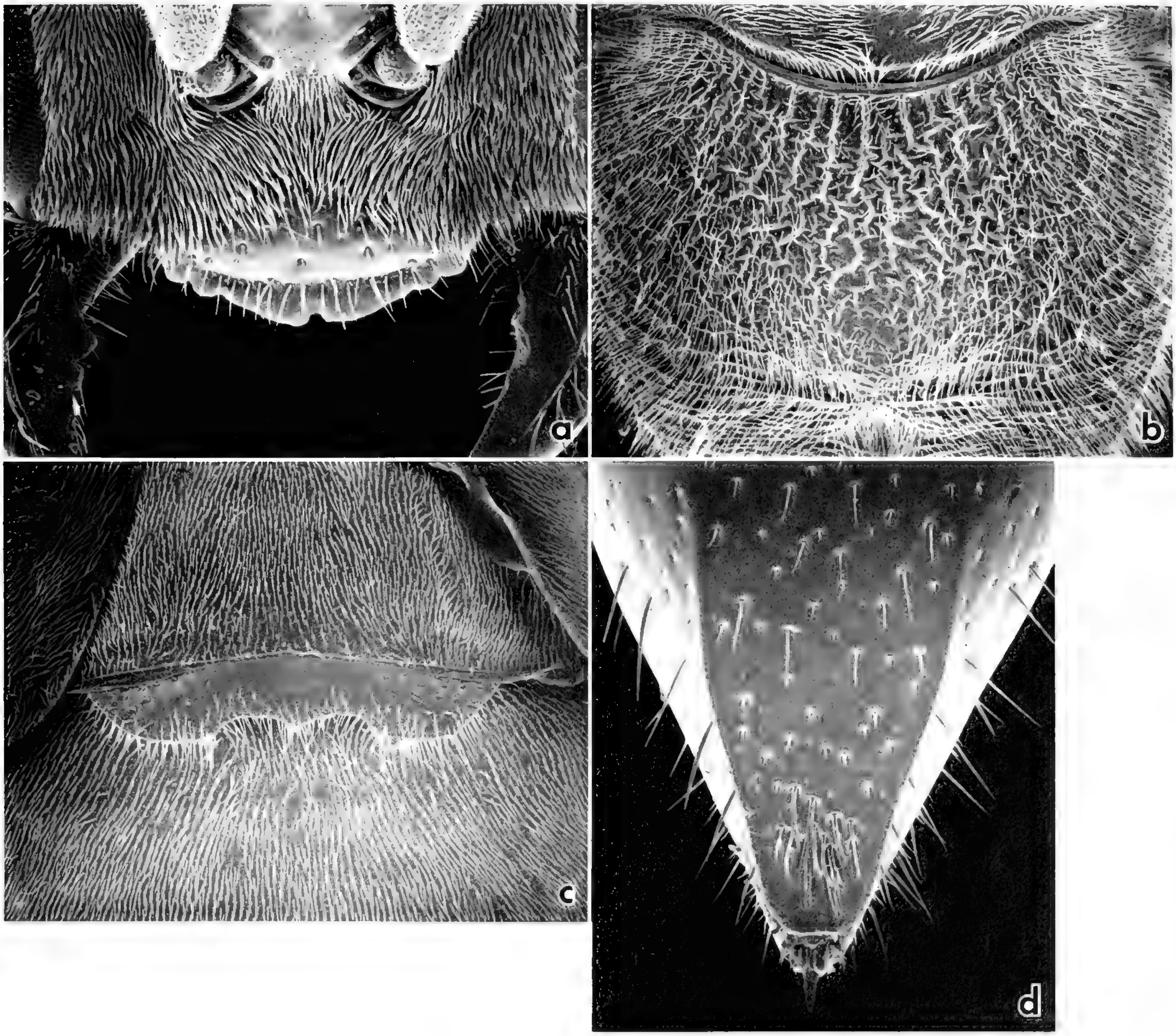

FIGURE 128 *Tachysphex belfragei* (Cresson), female: a—clypeus; b—propodeal dorsum; c—apex of sternum I and base of sternum II; d—pygidial plate

antennae with her mandibles. The prey was carried directly into the nest (Kurczewski did not say it explicitly, but this description suggests that the nest is permanently open during the provisioning period). The cell was stocked with four prey, and an egg was placed "across the throat" of one of them. The nest was nearly vertical, 10 cm deep.

GEOGRAPHIC DISTRIBUTION (Fig. 130).—Eastern United States (except Florida) west to 100th meridian, north to Virginia and Wisconsin.

MATERIAL EXAMINED.—70♀, 33♂ (CNC, CU, FMNH, INHS, ISU, KU, MCZ, MPM, UAF, UCD, UGA, UMMZ, UMSP, USNM)

RECORDS.—UNITED STATES: ARKANSAS: **Benton, Crawford, Washington:** —. DISTRICT OF COLUMBIA: Washington. GEORGIA: **Clarke:** Athens. ILLINOIS: **Champaign:** Urbana. **Kankakee:** Kankakee. **Macoupin:** Carlinville. **Morgan:** Jacksonville. IOWA: **Woodbury:** Sioux City. KANSAS: **Barton, Dickinson:** —. **Douglas:** 4 mi W Baldwin, Lawrence. **Pottawatomie:** Little Gobi. LOUISIANA: **St. Landry:** Opelousas. MISSOURI: **Barry:** Eagle Rock. **Boone:** Columbia. **Henry:** Clinton. **St. Louis:** St. Louis. NEBRASKA: **Holt:** Goose Lake. **Lancaster:** Lincoln. NORTH CAROLINA: **Durham:** Durham. **Wake:** Raleigh. SOUTH CAROLINA: **Pickens:** Clemson. TEXAS: **Bexar:** San Antonio. **Bosque:** —. **Hall:** 3 air mi W Estelline. **Kimble:** Junction. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **Lee:** Fedor. **San Patricio:** 5 mi N Sinton. VIRGINIA: Shenandoah National Park. WISCONSIN: **Grant:** Wisconsin.

Tachysphex krombeiniellus Pulawski

(Figures 131, 132)

Tachysphex krombeiniellus Pulawski, 1982:41, ♀, ♂. Holotype: ♀, Florida: Levy Co.: no specific locality (USNM).—Noonan 1984:6.

DIAGNOSIS.—*Tachysphex krombeiniellus* has a basally red gaster and red tibiae, and its thoracic vestiture is short and does not obscure the integument (these characteristics are shared with *belfragei*, some females of *aequalis*, and many males of *mundus*). The evenly microareolate propodeal dorsum separates it from *belfragei* (in which the propodeal dorsum is rugose). In the fe-

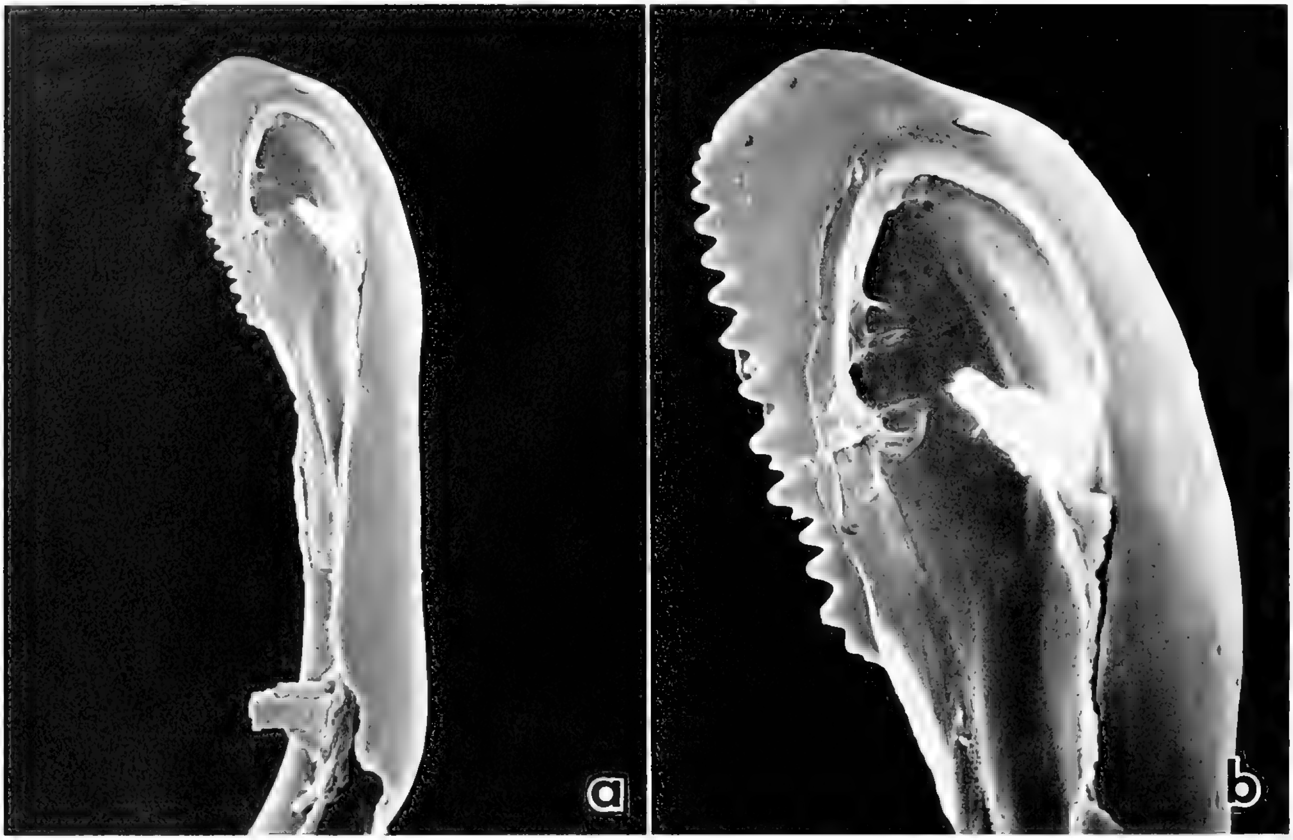

FIGURE 129. *Tachysphex belfragei* (Cresson): a—penis valve; b—same, apex.

male, the mesally expanded clypeal lip (see Fig. 128a) separates *krombeiniellus* from *aequalis* (and also the other species of the group except *belfragei*). In the male, the hindfemur is red in the apical third, the mesothoracic vestiture is golden or has a golden tinge, the vertex setae are appressed, and the apical (broad) portion of the penis valve is elongate (Fig. 131) (in *mundus*, the hindfemur is black, the mesothoracic vestiture is silvery, the vertex setae are erect or inclined, at least partly, and the apical portion of the penis valve is short, Fig. 121g, h).

DESCRIPTION.—Mesothorax evenly, minutely punctate, punctures subcontiguous; mesopleural punctures shallow, indistinct. Scutum roundly prominent posterolaterally. Propodeal dorsum evenly microareolate; side microsculptured, partly ridged in some specimens. Terga densely micropunctate.

Setae appressed on vertex, meosthorax, and femora, integument easily visible. Scutal setae oriented posterad.

Terga I–IV silvery fasciate apically. Tibiae and tarsi red. Wings weakly infumate.

♀.—Labrum with small, median notch. Clypeal bevel equal to basomedian area or slightly shorter; lip broadened mesally, emarginate mesally, with one or two lateral incisions on each side. Dorsal length of flagellomere I 1.8–2.0× apical width. Vertex punctures less than one diameter apart. Basal platform of sternum II straight or biemarginate apically. Pygidial plate narrow, densely setose apically. Tarsomere V without spines on venter or margins. Length 9–10 mm.

Setae length about 1.0 MOD along hypostomal carina and on propodeal dorsum.

Gastral segments I and II red, remainder black. Forefemur black (except apically) or red on apical third; mid- and hindfemur black (except on apical third) or red.

♂.—Clypeal bevel almost flat, shorter than basomedian area; lip broadly arcuate, distance between its corners equal to 0.9–1.0 of clypeal length. Dorsal length of flagellomere I 1.2–1.6× apical width. Vertex punctures fine, subcontiguous. Sterna densely punctate and pubescent throughout, but not fasciate apically; sterna III–VI with graduli. Length 7–10 mm. Penis valve: Figure 131.

Setae length about 0.5 MOD along hypostomal carina, 0.5–1.0 MOD on propodeal dorsum.

Tergum I red (except basally), usually also segment II; remainder black. Femora black, red apically (hindfemur red on apical third). Frontal vestiture golden or with golden tinge.

LIFE HISTORY.—Two females from Lincoln, Nebraska (UNL), were collected on flowers of *Solidago missouriensis* Nutt. (=*S. glaberrima* Martens).

GEOGRAPHIC DISTRIBUTION (Fig. 132).—Mainly central United States between southern Texas and North Dakota, west to 105th meridian, but also South Carolina, Arkansas, and Florida.

MATERIAL EXAMINED.—48♀, 27♂ (CAS, CIS, CU, FSCA, INHS, KU, MCZ, MPM, NYSU, UCD, UFG, UGA, UMSP, UNL, USNM)

RECORDS.—UNITED STATES: ARKANSAS: **Mississippi:** —. COLORADO: **Yuma:** Yuma. FLORIDA: **Alachua:** junction of roads 225 and 340, Monteoca (11 mi NW Gainesville). **Gadsden:** Quincy. **Leon:** Tall Timbers Research Station **Levy:** —. KANSAS: **Graham:** Hill City. **Pottawatomie:** Blackjack. **Reno:** Hutchinson. MINNESOTA: **Goodhue:** Cannon Falls. **Scott:** Barden (between Savage and

FIGURE 130. Geographic distribution of *Tachysphex belfragei* (Cresson) and *maya* sp. n

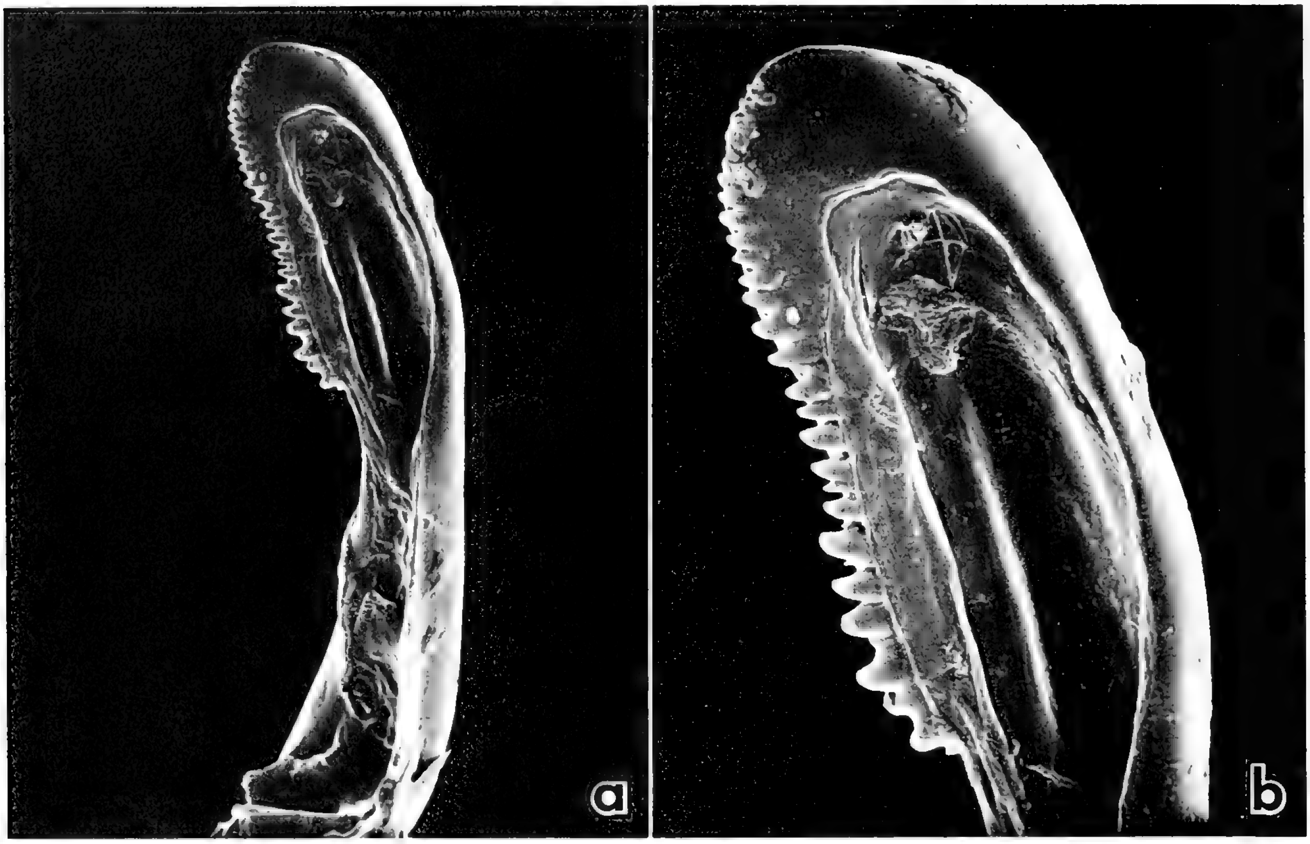

FIGURE 131. *Tachysphex krombeiniellus* Pulawski: a—penis valve; b—same, apical portion.

Shakopee). NEBRASKA: **Blaine:** Halsey, Dunning. **Box Butte:** Alliance. **Dawson:** Gothenburg. **Douglas:** Omaha. **Hall:** 6 mi W Cairo. **Keith:** Ogallala. **Lancaster:** Lincoln. **Lincoln:** North Platte. **Nance:** Genoa. **Thomas:** Thedford. NORTH DAKOTA: **Ransom:** 7 mi SE Sheldon. **Richland:** 11 mi W Walcott. SOUTH CAROLINA: **Aiken:** New Ellenton. SOUTH DAKOTA: **Bennett:** 24 mi E Martin. **Todd:** 20 mi S Mission. TEXAS: **Atascosa:** Pleasanton. **Jim Hogg:** 7 mi S Hebbronville. **Kleberg:** Baffin Bay 20 mi SE Kingsville. **Potter:** 5 mi N Amarillo. WISCONSIN: **Vernon:** Genoa.

Tachysphex menkei Pulawski

(Figures 133, 134)

Tachysphex menkei Pulawski, 1982:41, ♀, ♂. ! Holotype: ♀, California: San Diego Co.: Borrego Valley (UCD).

DIAGNOSIS.—*Tachysphex menkei* can be easily recognized by the woolly setae of the head and thorax (Fig. 133b); the finely, sparsely punctate scutum, scutellum, mesopleuron, and propodeal side; the largely impunctate, red gaster; and the glabrous male sterna III–VI.

DESCRIPTION.—Midscutal and mesopleural punctures fine, many diameters apart, interspaces aciculate. Scutal hindcorner rounded, not prominent. Propodeal dorsum opaque, evenly microareolate (indistinctly in some specimens); side weakly shiny, in most specimens with minute punctures that are several diameters apart.

Mesopleural and femoral vestitures suberect, integument easily visible. Scutal setae oriented posterad.

Terga I–III (I–IV in some males) silvery fasciate apically; fasciae weak in female.

♀.—Labrum shallowly emarginate. Clypeus (Fig. 133a): bevel equal to basomedian area or much longer; lip not emarginate or with rudimentary emargination mesally, with one or two lateral incisions on each side. Dorsal length of flagellomere I 2.1–2.5× apical width. Vertex punctures fine, more than one diameter apart. Terga II–V without micropunctures (except laterally). Pygidial plate moderately broad. Tarsomere V without spines on venter and margins. Length 9.0–10.5 mm.

Erect setae of head and thorax woolly (Fig. 133b); setae length (in MOD): 1.0–1.2 on vertex, 2.5–3.0 along hypostomal carina, 2.0–2.5 anterolaterally on scutum, 1.6–1.8 on propodeal dorsum, and 1.2–1.6 on midfemoral venter.

Gaster red. Femora black or hindfemur largely red; tibiae black or largely red (including inner side of foretibia); tarsi red.

♂.—Clypeus (Fig. 133c): bevel convex, shiny, equal to basomedian area or shorter; lip almost straight, with rectangular or obtuse corner. Dorsal length of flagellomere I 1.5–1.9× apical width. Vertex punctures fine, well defined, one to four diameters apart. Terga III–V without micropunctures (except basally in some specimens); sterna III–VI impunctate, glabrous (at least mesally), without graduli or transverse sulcus, not fasciate apically. Length 5.5–10.0 mm.

Erect setae along hypostomal carina and on thorax woolly (only weakly so in smallest specimens); setae length (in MOD): 1.0–1.2 on vertex, 1.6–2.5 along hypostomal carina and anterolaterally on scutum, 1.4–2.0 on propodeal dorsum, 1.0 in midfemoral venter. Apical depression of terga IV and V glabrous.

Gaster red, but tergum I black basally; apical terga brownish

FIGURE 132. Geographic distribution of *Tachysphex krombeiniellus* Pulawski.

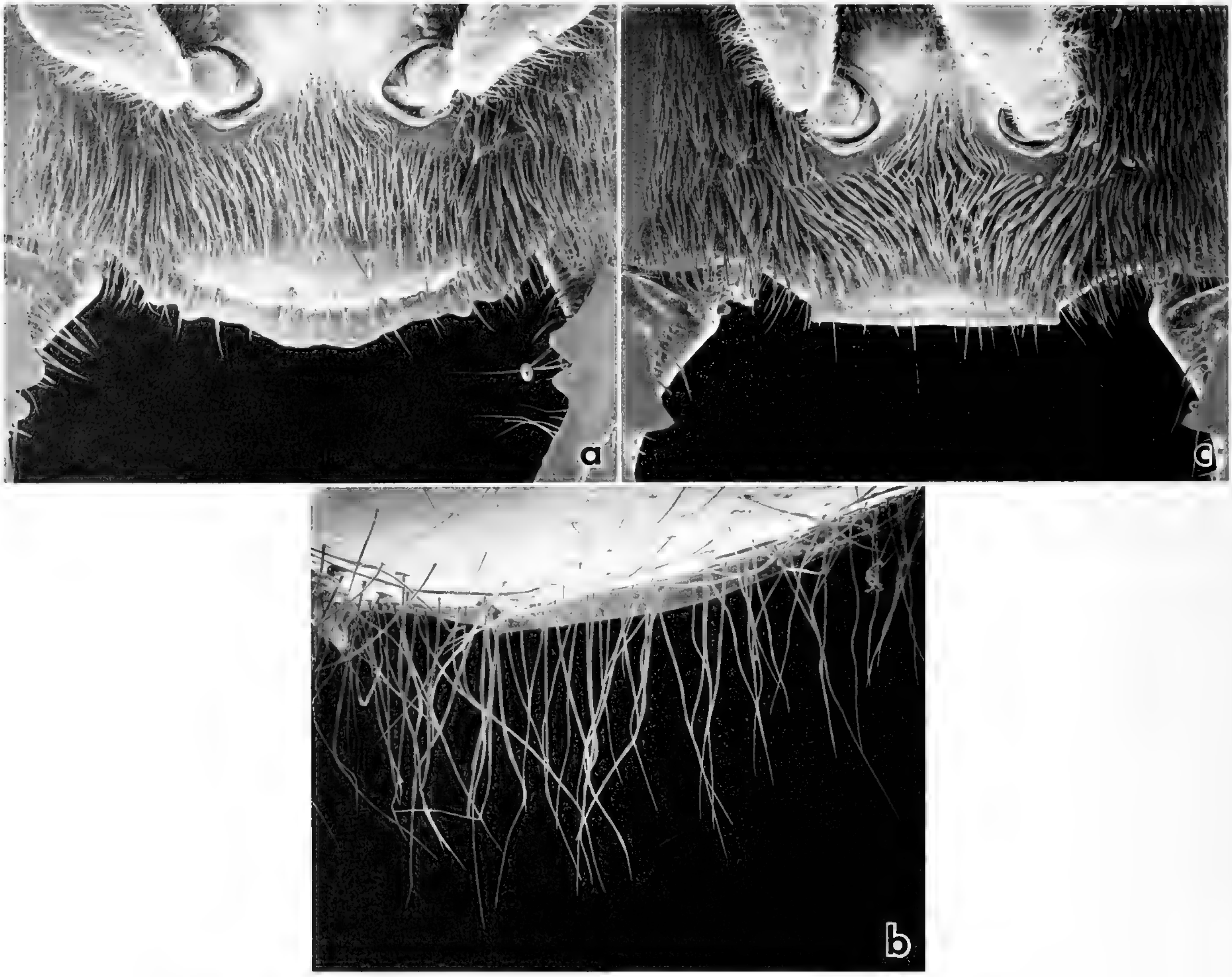

FIGURE 133 *Tachysphex menkei* Pulawski: a—female clypeus; b—female setae adjacent to hypostomal carina; c—male clypeus.

in some specimens. Femora black, tibia I red on inner face, tibia II and III black or largely red; tarsi red. Frontal vestiture golden, but silvery in smallest specimens.

LIFE HISTORY.—A paratype female is pinned with her prey: a young nymph of a decticine katydid, probably *Eremopedes* sp., det. A. B. Gurney.

GEOGRAPHIC DISTRIBUTION (Fig. 134).—Desert areas from southwestern Texas to southern California.

MATERIAL EXAMINED.—13♀, 44♂ (ANSP, ASU, CAS, CNC, CSDA, LACM, MCZ, NSDA, UAT, UCD, UMMZ, USNM, USU).

RECORDS.—UNITED STATES: ARIZONA: **Graham:** Roper Lake State Park, 18 mi E Safford. **Maricopa:** 30 mi E Gila Bend. **Pima:** Silver Bell. **Pinal:** Boyce Thompson Arboretum 3 mi W Superior. **Santa Cruz:** Canelo. **Yavapai:** 10 mi NW Congress, Prescott, 5 mi N Wickenburg. **Yuma:** 5 mi SW Bouse. CALIFORNIA: **Imperial:** 30 mi NE Glamis. **San Bernardino:** Adelanto. **San Diego:** Borrego Valley. **Riverside:** Andreas Canyon, Palm Springs. NEVADA: **Clark:** Cabin Creek S Mesquite. **Lincoln:** Garden Wash (ca. 12 mi E Carp). NEW MEXICO: **Otero:** Alamogordo. **Socorro:** Bernardo. TEXAS: **Brewster:** Alpine, Big Bend National Park (Dugout Well, Nine Point Draw, Santa Elena Canyon). **El Paso:** Tornillo. **Hudspeth:** McNary. **Presidio:** 3 mi E Presidio. UTAH: **Washington:** Paradise Canyon.

Tachysphex maya sp. n.
(Figures 130, 135)

DERIVATION OF NAME.—Named after the Maya Indians of Central America; noun in apposition.

DIAGNOSIS.—*Tachysphex maya* is unique among the New World species of the *brullii* group in having the propodeal dorsum setae oriented anterad on a broad, median zone that extends from the base to apex (the lateral setae are oriented posterad). Within the North American species of the *brullii* subgroup, *maya* is unique in having conspicuous mesopleural punctures. It resembles members of the *pompiliformis* group that have a similar orientation of the propodeal setae, but the female has the specialized apical tarsomere characteristic of the *brullii* group; the male has a distinctive combination of narrow vertex (width about 0.7 of length) and punctate mesopleuron.

DESCRIPTION.—Vertex with median sulcus that extends posterad from postocellar impression. Scutal hindcorner not prominent. Punctures: nearly contiguous on scutum; on mesopleuron

well defined, large to fine, less than one diameter apart anteriorly and up to two or three diameters apart posteriorly. Propodeal dorsum microareolate; side impunctate anteriorly, punctate posteriorly. Terga densely micropunctate.

Setae: on vertex inclined (erect on postocellar impression), about 0.7 MOD long; on hypoepimeral area erect or nearly so, inclined on remaining mesopleuron; on propodeal dorsum oriented obliquely anterad on broad, median area that extends from base to apex, and oriented posterad on lateral, narrow area; appressed or nearly so on femora; underlying vestiture easily visible. Scutal setae oriented posterad.

Head, thorax, and legs black, tibial apex and tarsus red, also inner face of foretibia in some males (one from Cuernavaca, one from Junquillal Beach). Gaster red. Terga I–III fasciate apically, male tergum IV with interrupted fascia. Wings weakly infumate.

♀.—Labrum emarginate mesally. Clypeus (Fig. 135a): bevel longer than basomedian area; lip arcuate, shallowly emarginate mesally, with two lateral incisions on each side. Dorsal length of flagellomere I 2.0–2.2× apical width. Vertex punctures up to one to two or two to three diameters apart mesally. Pygidial plate smooth or alutaceous, sparsely punctate. Tarsomeres V without spines on venter, but outer margin at midlength with one (foretarsus) or two (mid- and hindtarsus) spines in specimen from Guadalajara area; these spines are evanescent or absent in female from Tehuantepec area. Length 9.5–11.5 mm.

Setae length 1.3 MOD along hypostomal carina and on propodeal dorsum.

Clypeal and frontal vestiture silvery, with golden tinge.

♂.—Clypeus (Fig. 135b): bevel convex, shorter than basomedian area; lip arcuate, with prominent corners; distance between corners equal to clypeal midline. Dorsal length of flagellomere I 1.4–1.6× apical width. Vertex punctures varying from less than one diameter apart up to two or three diameters apart mesally. Sterna densely punctate and pubescent mesally, sternal hindmargins without setal fasciae; sterna III–VI with graduli. Length 9.0–9.5 mm. Penis valve: Figure 135c.

Setae length 1.3 MOD along hypostomal carina and about 1.5 MOD on propodeal dorsum.

Clypeal and frontal vestiture golden.

Geographic Distribution (Fig. 130).—Mexico south of the Tropic of Cancer to Costa Rica.

Collecting Period.—2 March to 23 May.

Material Examined.—Holotype: ♂, Mexico: Chiapas: Villa Flores, 2 March 1953, RCB and EIS (UCD).

Paratypes (2♀, 4♂): MEXICO: **Jalisco:** 40 mi NE Guadalajara, 23 May 1956, H. A. Scullen (1♀, UCD). **Morelos:** Cuernavaca, 5 Mar 1969, HEE and D. M. Anderson (1♂, CU). **Oaxaca:** 62 mi W Tehuantepec, 5 Mar 1985, LAS and R. Miller (1♀, CAS). **Sinaloa:** 9 mi E Chupaderos, 19 Mar 1962, LAS (1♂, CAS).

COSTA RICA: **Guanacaste:** Junquillal Beach, 8 Mar 1976, RMB (1♂, UCD); Río Corbici near Cañas, 8 Mar 1976, RMB (1♂, UCD).

Tachysphex acanthophorus Pulawski

(Figures 136, 137)

Tachysphex acanthophorus Pulawski, 1982:39, ♀, ♂. ! Holotype: ♀, Arizona, Cochise Co.: Willcox (UCD)

Diagnosis.—*Tachysphex acanthophorus* has laterally oriented midscutal setae, a character also found in *armatus* and *cocopa*. The female has a distinctive tarsomere V: one or two subapical spines are present on each lateral margin (Fig. 136b), and in most specimens also one or several midventral spines (Fig. 136b); there are no basoventral spines (that are present in *armatus*). An identical tarsomere V is also found in *cocopa* and

Figure 134. Geographic distribution of *Tachysphex menkei* Pulawski

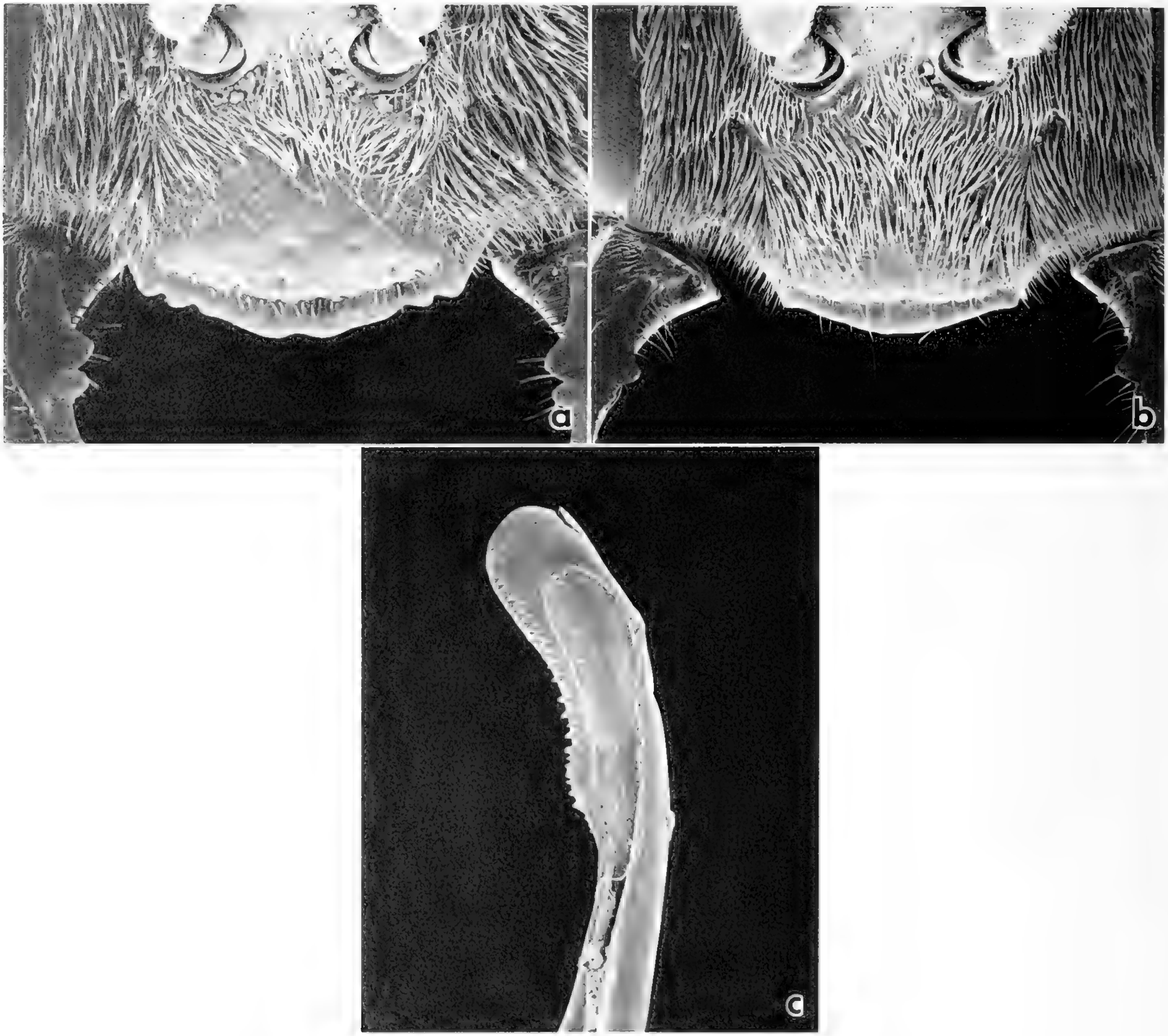

FIGURE 135. *Tachysphex maya* sp. n a—female clypeus; b—male clypeus; c—penis valve

the South American *spinulosus* Pulawski, and the lateral spines are also found in most *aequalis*. However, the almost asetose pygidial plate separates *acanthophorus* from *cocopa* (in which the plate is densely setose throughout); the mesopleural vestiture is dense, partly obscuring integument (integument easily visible in *aequalis*); the gaster is red (at least basally); and the femora are black or the hindfemur is partly reddish (in *spinulosus*, the gaster is black, and the mid- and hindfemora are red).

Males of *acanthophorus* have a very narrow clypeal lip and lack a clypeal bevel (Fig. 136d); a transverse sulcus (visible only when sterna are fully extended) is present on sterna III–VI (Fig. 136e); and graduli are absent. These characters separate *acanthophorus* from all other species of the *brullii* group except *armatus* and *cocopa*. Males of these three species are very similar, and I was unable to separate them with certainty. The differences between males of *acanthophorus* and *cocopa* are unknown, but *acanthophorus* is widely distributed in southwestern United States and northern Mexico, and *cocopa* is known from only a few localities in southern Arizona, southern California, and northern Sonora, Mexico. The differences found between *acanthophorus* and *armatus* may actually be individual, and not specific. In *acanthophorus*, sternum II is somewhat swollen along the front margin of the apical depression, and the mesopleural integument is obscured by vestiture or nearly so; in *armatus*, the sternal surface is flat, and the mesopleural integument is easily visible.

DESCRIPTION.—Scutal and scutellar punctures minute, even, subcontiguous; scutal hindcorners roundly prominent. Propodeal dorsum microareolate, side minutely, indistinctly punctate (puncture evanescent in some specimens).

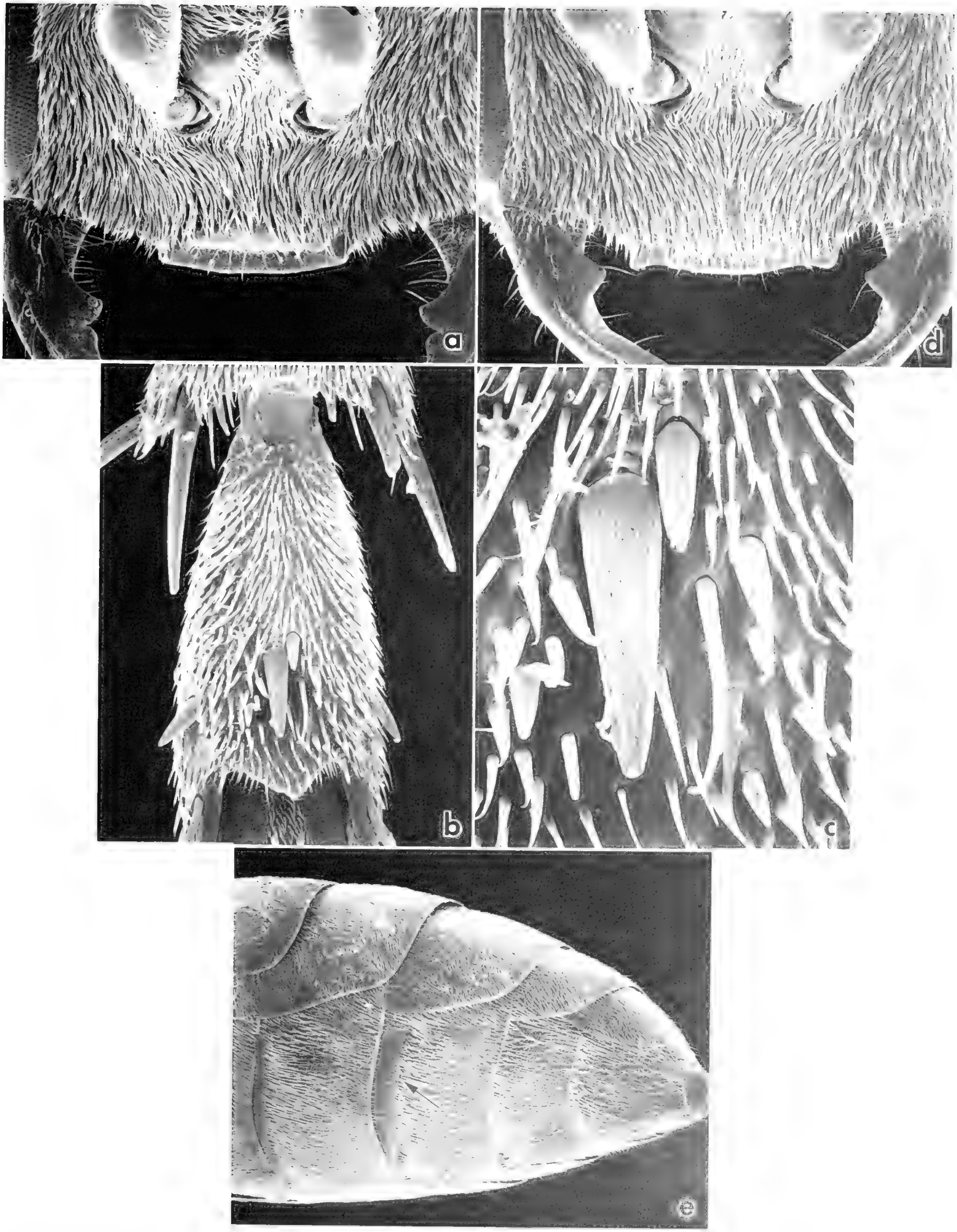

FIGURE 136. *Tachysphex acanthophorus* Pulawski: a—female clypeus, b—female hindtarsomere V, ventral view, c—same, central cluster of spines, d—male clypeus, e—male gaster, oblique view (arrow indicates transverse sulcus)

FIGURE 137 Geographic distribution of *Tachysphex acanthophorus* Pulawski

Vestiture appressed on vertex, mesothorax, and femora; sculpture partly obscured on mesopleuron, largely or completely so on forefemoral venter. Midscutal setae oriented laterad (except setae on midline that are oriented posterad).

Gaster red or (some individuals) terga IV–VI dark (IV–VII in male); terga I–IV (I–V in some males) silvery fasciate apically. Wings hyaline.

♀.—Labrum at most weakly emarginate. Clypeal bevel almost as long as basomedian area to absent (some Texas and New Mexican individuals); lip entire or (some specimens) with one or two minute, lateral incisions on each side. Dorsal length of flagellomere I 1.6–2.0 × apical width. Vertex punctures minute, even, about one diameter apart or less, interspaces dull. Mesopleural punctures minute, dense, indistinct in some specimens. Tergal micropunctures dense. Pygidial plate moderately broad, with appressed setae. Forebasitarsus with five to nine rake spines. Tarsomere V with two subapical spines (one in some specimens) on each lateral margin, usually with central cluster of spines on venter (Fig. 136b, c). Length 5.5–7.0 mm.

Setae length about 1.2–1.4 MOD long along hypostomal carina and on propodeal dorsum.

Femora black or hindfemur partly reddish; tibiae black or largely red; tarsi red or (some specimens) black basally. Wings hyaline.

♂.—Clypeal bevel absent; lip narrower than in related species (except *armatus*), almost straight to weakly arcuate, corners obtuse to sharp, prominent. Dorsal length of flagellomere I 1.2–1.6 × apical width. Vertex punctures minute, indistinct, less than one diameter apart, interspaces microsculptured. Mesopleuron microsculptured, somewhat shiny, practically impunctate. Terga and sterna densely punctate and pubescent throughout; sterna III–VI (except laterally) with straight, transverse sulcus (which is visible only when segments are fully extended). Length 5.5–7.0 mm.

Setae length about 1.0 MOD along hypostomal carina and on propodeal dorsum.

Femora black. Tibia I red (at least on inner face), tibia II and III black or red; tarsi red. Frontal vestiture golden above, silvery below.

GEOGRAPHIC DISTRIBUTION (Fig. 137).—Xeric areas of southwestern United States and northern Mexico.

MATERIAL EXAMINED.—182♀, 203♂, 1 gynandromorph.

RECORDS.—UNITED STATES: ARIZONA: **Cochise:** Apache (also 1 mi E), Bowie, 7 mi SE Dos Cabezas, Douglas (also 2 mi E), Hereford, Portal (also 2 mi E, 2 mi S, 2 mi NE, 6.5 mi SE), Tombstone, Willcox. **Graham:** Roper Lake State Park (6 mi S Safford). **Maricopa:** 5 mi N Aguila, Phoenix, Rainbow Valley, Tempe, 5 mi SE Wickenburg. **Pima:** 30 mi SE Ajo, Continental, Sabino Canyon (Santa Catalina Mts.), Silver Bell, Tucson. **Pinal:** 5 mi NW Coolidge, Picacho Pass, Superior (Boyce Thompson Arboretum). **Yuma:** Palm Canyon, Parker, 7 mi S Quartzsite. CALIFORNIA: **Imperial:** Brawley, Hot Mineral. **Inyo:** Antelope Springs (8 mi SW Deep Springs), Deep Springs, Tecopa. **Riverside:** Blythe (also 12 mi N, 18 and 20 mi W), 12 mi W Desert Center, Indio, 3.5 mi S Palm Desert. **San Bernardino:** Amboy, 6 mi S Kelso. **San Diego:** Borrego, Torrey Pines State Park. **Tulare:** Lemon Cove, Three Rivers. COLORADO: **Bent:** Hasty. NEVADA: **Clark:** Sandy. **Mineral:** Luning. **Nye:** Mercury. NEW MEXICO: **Dona Ana:** Las Cruces, Leasburg Dam State Park. **Eddy:** 15.5 mi W Artesia. **Grant:**25 mi E Lordsburg. **Hidalgo. Luna:** Columbus, 10 mi N Deming. **Otero:** White Sands National Monument. **Quay:** Tucumcari. **Socorro:** La Joya (20 mi N Socorro). TEXAS: **Bexar:** —. **Brewster:** Alpine, Big Bend National Park (Boquillas, Nine Point Draw, Rio Grande), Glenn Spring. **Crockett:** Fort Lancaster State Historical Park. **Duval:** 18 mi N San Diego. **El Paso:** 3 mi E Fabens. **Guadalupe:** Seguin. **Hidalgo:** McAllen Botanical Garden. **Hudspeth:** Fort Hancock, McNary, Sierra Blanca. **Presidio:** 3 mi E Presidio (also 11 mi N). UTAH: **Emery:** Bell Canyon in San Rafael Ridge, Wild Horse Creek W Goblin Valley. **Garfield:** Lake Powell (4 air mi NNW Bullfrog), Shootaring Canyon. **Washington:** Leeds Canyon, Paradise Canyon, St. George, Toquerville, Zion National Park.

MEXICO: **Baja California Sur:** 44 km S La Paz, 4 mi WSW Miraflores, Rancho Vinateria (22 km W Loreto, Sierra de la Giganta). **Chihuahua:** 15 mi S Chihuahua

Nuevo León: Vallecillo. **Sinaloa:** Culiacán, S Lorenzo, Mazatlán (also 2.5 and 5 mi N). **Sonora:** Alamos (also 10 mi SW), near Cucurpe, Desemboque, 20 mi S Estación Llano, Guaymas, 5 mi S Magdalena, Minas Nuevas, 10 mi E Navajoa, San Carlos (also 6 km NNW). **Tamaulipas:** Sierra Picachos.

Tachysphex armatus Pulawski

(Figures 138, 139)

Tachysphex armatus Pulawski, 1982:40, ♀, ♂. ! Holotype: ♀, Nevada: Clark Co.: Sandy (UCD).

Diagnosis.—The female of *armatus* is unique among the North American *Tachysphex* in having basoventral spines on the tarsomere V (Fig. 138). Otherwise it is similar to *acanthophorus* and *cocopa* with which it shares transversely oriented midscutal setae and also other structures of the tarsomere V: one to several midventral spines and one or two preapical spines on each lateral margin. The pygidial plate of *armatus* is almost asetose (pygidial plate densely setose throughout in *cocopa*).

The male of *armatus* is very similar to *acanthophorus*. See that species for differences.

Description.—Scutal and scutellar punctures fine, even, subcontiguous; scutal hindcorner roundly prominent. Propodeal dorsum microareolate; side weakly microsculptured, shiny, at most with inconspicuous punctures that are two to three diameters apart.

Vestiture appressed on vertex, mesothorax, and femora, dense but not obscuring sculpture on mesopleuron and forefemoral venter. Midscutal setae oriented laterad (except setae on midline which are oriented posterad). Setae length about 0.8 MOD along hypostomal carina and 0.8–1.2 MOD on propodeal dorsum.

Gaster red; terga I–IV silvery fasciate apically. Wings hyaline.

♀.—Labrum not emarginate. Clypeal bevel equal to basomedian area or shorter; lip evenly arcuate, without mesal notch or lateral incisions. Dorsal length of flagellomere I 1.9–2.1 × apical width. Vertex dull, minutely, evenly punctate, punctures less than one diameter apart. Mesopleuron microsculptured, impunctate. Terga I–III densely micropunctate. Pygidial plate broad, with a few, sparse setae. Foretarsomere with seven to nine rake spines. Tarsomere V with basal spines ventrally and laterally, with one to three central spines on venter, with one or two preapical spines on each lateral margin (Fig. 138). Length 7.0–9.5 mm.

Legs black, tarsal apex red; inner face of foretibia reddish in some individuals.

♂.—Clypeal bevel absent; lip narrow, as in *acanthophorus*, almost straight, lateral corners acute (prominent) or obtuse. Dorsal length of flagellomere I 1.5–1.7 × apical width. Vertex microsculptured, punctures minute, less than one diameter apart. Mesopleuron microsculptured, somewhat shiny, practically impunctate. Terga and sterna densely punctate and pubescent throughout. Sterna III–VI (except laterally) with transverse sulcus (which is visible only when segments are fully extended). Length: 7.0–7.5 mm.

Femora black, tibiae dark with reddish zones, inner face of foretibia red, tarsi red. Frontal vestiture silvery, with golden tinge before midocellus.

Geographic Distribution (Fig. 139).—Desert areas from southwestern Texas to California, also Baja California.

Material Examined.—28♀, 23♂ (CAS, CIS, CNC, CSU, LACM, SDNH, UCD, UCR, USNM, USU).

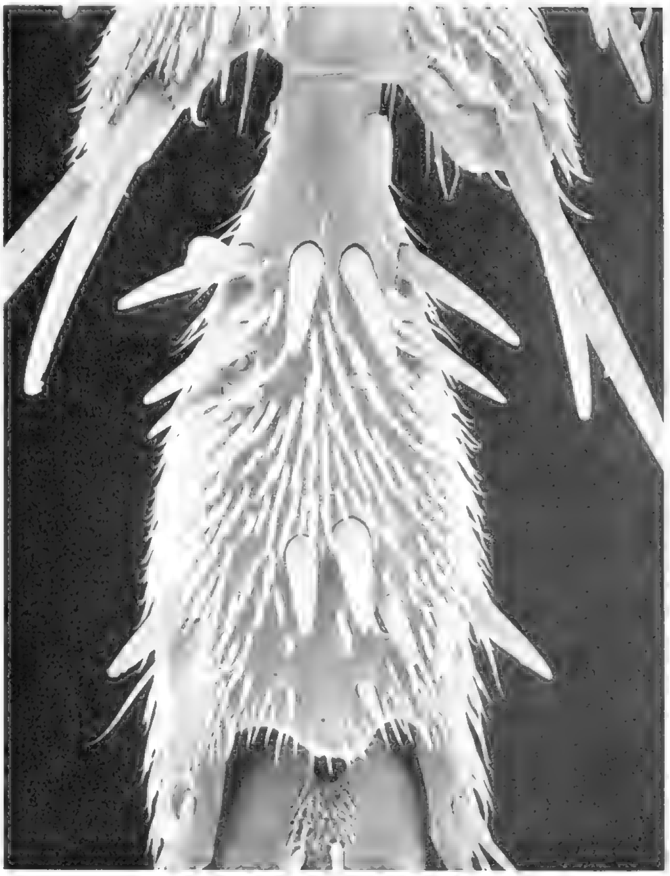

Figure 138. *Tachysphex armatus* Pulawski: a—female hindtarsomere V, ventral view.

Records.—UNITED STATES: ARIZONA: **Maricopa:** 10 mi E Gila Bend, Phoenix, 5 mi SE Wickenburg. **Pima:** Tucson. CALIFORNIA: **Inyo:** 12 mi N and 10 mi W Eureka Dunes. **Riverside:** Joshua Tree National Monument (36 road mi S Twentynine Palms). **San Diego:** San Diego. NEVADA: **Clark:** Sandy. **Lincoln:** Alamo. NEW MEXICO: **Dona Ana:** Leasburg Dam State Park. **Socorro:** Rio Salado 5 mi W Interstate Highway 25. TEXAS: **Brewster:** Big Bend National Park (Nine Point Draw). **Hudspeth:** Fort Hancock, McNary. **Presidio:** 11 mi N Presidio. UTAH: **Washington:** Leeds Canyon.

MEXICO: **Baja California Norte:** 38 km S Rosarito, 220 km S Tijuana. **Baja California Sur:** 7 mi SW La Paz, 13.5 mi S Loreto.

Tachysphex cocopa sp. n.

(Figures 139, 140)

Derivation of Name.—Named after the Cocopa Indians of the Yuman linguistic family, who lived near the mouth of Colorado River; a noun in apposition.

Diagnosis.—*Tachysphex cocopa* is the only *Tachysphex* in which the pygidial plate of the female is totally covered with setae (Fig. 139). The presence of only five rake spines on the female forebasitarsus is an additional recognition feature. Otherwise the species is very similar to *acanthophorus*. Diagnostic characters are unknown for the male (see Discussion below).

Description.—Scutal and scutellar punctures fine, even, nearly contiguous. Scutal hindcorners rounded, not prominent. Propodeal dorsum microareolate; side micropunctate, shiny.

Vestiture appressed on vertex, mesothorax, and femora, largely obscuring sculpture on mesopleuron and forefemoral venter.

FIGURE 139. Geographic distribution of *Tachysphex armatus* Pulawski and *cocopa* sp. n.

Setae length about 0.8 MOD along hypostomal carina, about 1.0 MOD on propodeal dorsum.

Gaster red. Frontal vestiture silvery; terga I–IV silvery fasciate apically, tergum V with some silvery tomentum laterally. Wings hyaline.

♀.—Labrum not emarginate. Clypeal bevel shorter than basomedian area; lip evenly arcuate, without mesal notch or lateral incisions. Dorsal length of flagellomere I 1.7–2.0× apical width. Vertex minutely, evenly punctate, punctures less than one diameter apart. Terga I–III densely micropunctate. Pygidial plate (Fig. 140) broad, densely punctate, and setose. Forebasitarsus with five rake spines. Tarsomere V with three or (some specimens) four preapical spines on each lateral margin, with a central group of spines on venter. Length 7.0–8.5 mm.

Fore- and midfemur black, hindfemur red or partly black; foretibia black except red at both ends and reddish on inner side; midtibia black, red on both ends, hindtibia red in continental specimens, largely black in specimens from Tiburón Island.

♂.—Clypeal bevel absent; lip arcuate, not prominent laterally. Dorsal length of tarsomere I 1.5× width. Vertex micropunctate, punctures less than one diameter apart. Mesopleuron microsculptured, somewhat shiny. Terga and sterna densely punctate and pubescent throughout. Sterna III–VI (except laterally) with transverse sulcus which is visible only when sterna are fully extended. Length 7 mm.

Femora black; tibiae black, except red basally and apically, foretibia reddish on inner side.

DISCUSSION.—Two males, collected together with females of *cocopa* on Isla Tiburón, Mexico, are indistinguishable from *acanthophorus* and may in fact be that species. However, I assign them to *cocopa*, as no females of *acanthophorus* are known from the island.

GEOGRAPHIC DISTRIBUTION (Fig. 139).—Arizona, southern California, and Sonora, Mexico.

COLLECTING PERIOD.—10 May to 11 July.

MATERIAL EXAMINED.—Holotype: ♀, Mexico: Sonora: SW part of Isla Tiburón, 10 May 1962, C. Bolinger (OSU, on permanent deposit to CAS, CAS Type #15916).

Paratypes (8♀, 2♂): UNITED STATES: ARIZONA: **Maricopa:** Phoenix, 18 May 1938, R. H. Crandall (1♀, UCD). CALIFORNIA: **Imperial:** Calexico, 11 July 1957, EIS (2♀, CAS; 1♀, UCD), 23 Sep 1957 (1♀, UCD).

MEXICO: **Sonora:** same data as holotype (2♀, 1♂ with gaster missing, CAS; 1♀, 1♂, OSU)

obscuripennis Subgroup

Female scutum and scutellum more or less flattened; outer side of foretibia without spines, with setae only; tarsomeres IV wider than long, obtusely emarginate apically; tarsomeres V angulate basoventrally in lateral view; claws asymmetrical (one claw in each pair being smaller), short, stout, arolium extending beyond their midlength; forebasitarsus with five to seven rake spines.

Prey consists of blattids. The subgroup is poorly represented in the Nearctic Region, and its species are limited to its southern part (Florida, southern Texas, and Sonora, Mexico). It is well represented in all other zoogeographic regions.

The three members of the subgroup share the following characters: vestiture not obscuring integument between antennal socket and orbit; scutum with well-defined punctures, its hind-

corner roundly prominent. Female labrum emarginate; forefemoral venter sparsely punctate, interspaces unsculptured or finely microsculptured; tarsomeres V with row of short spines on each lateral margin, apicoventral margin produced into lobe. Male vertex wider than long; tergum VII densely punctate.

Tachysphex inconspicuus (Kirby)

(Figures 141–143)

Tachytes inconspicuus Kirby, 1890:540, ♀, ♂. ! Lectotype: ♀, Brazil: Fernando de Noronha Island (BMNH), designated by Pulawski 1974*a*:74.—In *Tachysphex*. Pulawski 1974*a*:74 (full bibliography); Bohart and Menke 1976:274.

Tachysphex blatticidus Williams, 1941:197, ♀, ♂. ! Holotype: ♀, Trinidad and Tobago: Trinidad Island: St. Augustine (BMNH). Synonymized by Pulawski 1974*a*:74.

Diagnosis.—*Tachysphex inconspicuus* has a basal tooth (Fig. 141c) on the hindcoxa (tooth absent in *iridipennis*), and setae of the propodeal dorsum are erect or inclined posterad (basomedian setae oriented anterad in *alayoi*). The female hindfemur is slenderer (Fig. 141d) than in the other two, and the tarsomere IV is undulate apicoventrally, not produced into lobe (Fig. 142c, e). The male sterna are densely punctate and pubescent (sterna IV–VI almost impunctate and glabrous in *alayoi*, sparsely punctate in *iridipennis*), and the foretarsal rake is absent (preapical rake spines present on forebasitarsus in *iridipennis* and many *alayoi*). In most specimens the vertex setae are 1.0–1.5 MOD long (1.5–3.0 in the two other species), the propodeal side is not ridged, the clypeal lip of the female has two lateral incisions (Fig. 141a) (not incised in the other two), and the rake spines of the female foretarsus are 2.5–3.0× the basitarsal width (1.2–2.0× in the other two).

Description.—Frons dull, microsculptured. Vertex in most specimens with two swellings behind postocellar impression. Scutal and mesopleural punctures no less than one diameter apart. Axilla steplike. Punctures of mesothoracic venter about one diameter apart. Metapleuron in most specimens with longitudinal carina beneath flange, the latter broad. Propodeal dorsum rugose or longitudinally ridged (Fig. 141b), smooth apically in some specimens, carinate along hindmargin (also along lateral margin in some specimens); side punctate (punctures inconspicuous in some females), rarely ridged apicoventrally or (some males) largely rugose. Hindcoxa with prominent tooth basally (Fig. 141c).

Setae of propodeal dorsum erect or slightly inclined posterad (Fig. 141b).

Body black, tarsi red or reddish except black in Jamaican specimens. Terga I–IV or I–V silvery fasciate apically. Wings hyaline to infumate in female, slightly infumate in male.

♀.—Clypeus (Fig. 141a): bevel one-third to half length of basomedian area, indistinctly delimited from the latter; lip straight to slightly sinuate, with mesal notch, in most specimens with two lateral incisions. Dorsal length of flagellomere I 1.5–2.3× apical width. Vertex width 1.1–1.4× length. Punctures shallow on frons (inconspicuous in some specimens); dense to sparse on vertex; well defined to faint on mesopleuron (interspaces shiny); dense on tergum V (apical depression impunctate). Scutellum and postscutellum flattened but somewhat convex, scutum in many specimens longitudinally crenulate along hindmargin. Pygidial plate punctate, asetose, broad to (some specimens) narrow. Rake spines of forebasitarsus 2.5–3.0× width of basitarsus.

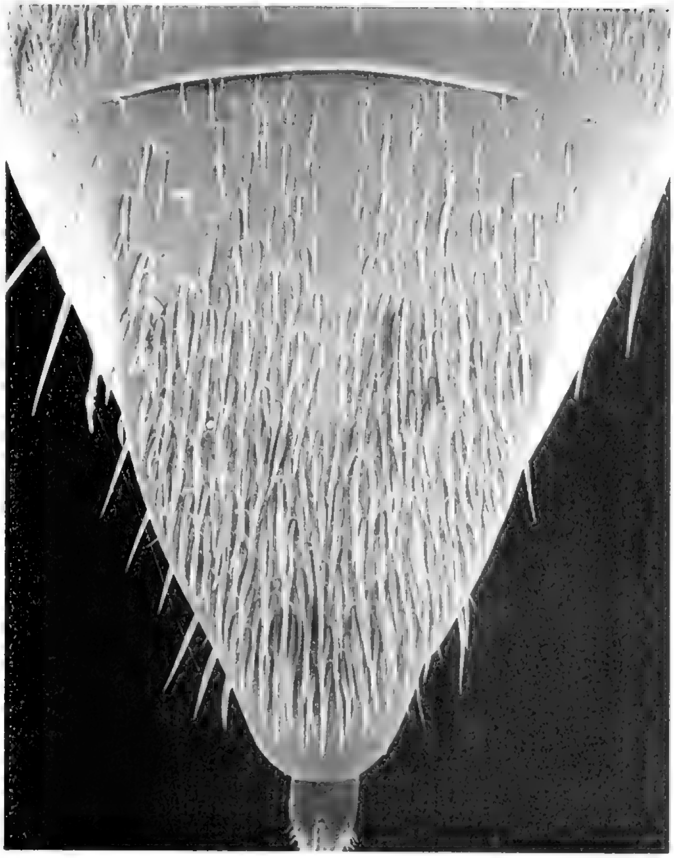

Figure 140. *Tachysphex cocopa* sp. n.: pygidial plate of female.

Hindfemur slender (Fig. 141d). Tarsomere IV (Fig. 142a–d): apical emargination weakly obtuse, its membrane exposed (hidden in other *Tachysphex*), apicoventral margin undulate, not expanded into a lobe. Tarsomere V: Figure 142e. Length 7.0–8.5 mm.

Setae erect, in most specimens 1.0–1.5 MOD long on vertex, about 1.0 MOD on scutum and midfemoral venter. Foretibia densely pubescent throughout.

♂.—Clypeus (Fig. 141e): bevel absent; lip varying: straight, broadly arcuate, or with obtuse, median projection; corners angulate but not prominent, slightly closer to orbit than to each other (rarely closer to each other). Dorsal length of flagellomere I 1.2–1.8× apical width. Frons punctate (only shallowly so in some individuals). Vertex width 1.3–1.7× length. Sterna densely punctate and pubescent throughout. Forefemoral notch glabrous. Foretarsus without rake. Length 5.5–8.0 mm.

Setae erect on vertex, suberect on scutum; 1.0–1.2 MOD long on vertex and scutum, about 0.6 MOD on midfemoral venter, at most 0.5 MOD on hindfemoral venter.

Variation.—In a female from Turrialba, Costa Rica (CAS), the clypeal lip is not incised laterally, and the vertex setae are 2.5 MOD long. Occasional specimens from Peru and Ecuador are similar. The rake spines may be unusually short in some South American females (see Pulawski 1974*a*).

Life History.—Available data were summarized by Pulawski (1974*a*). Females nest in sand and provision with adult roaches

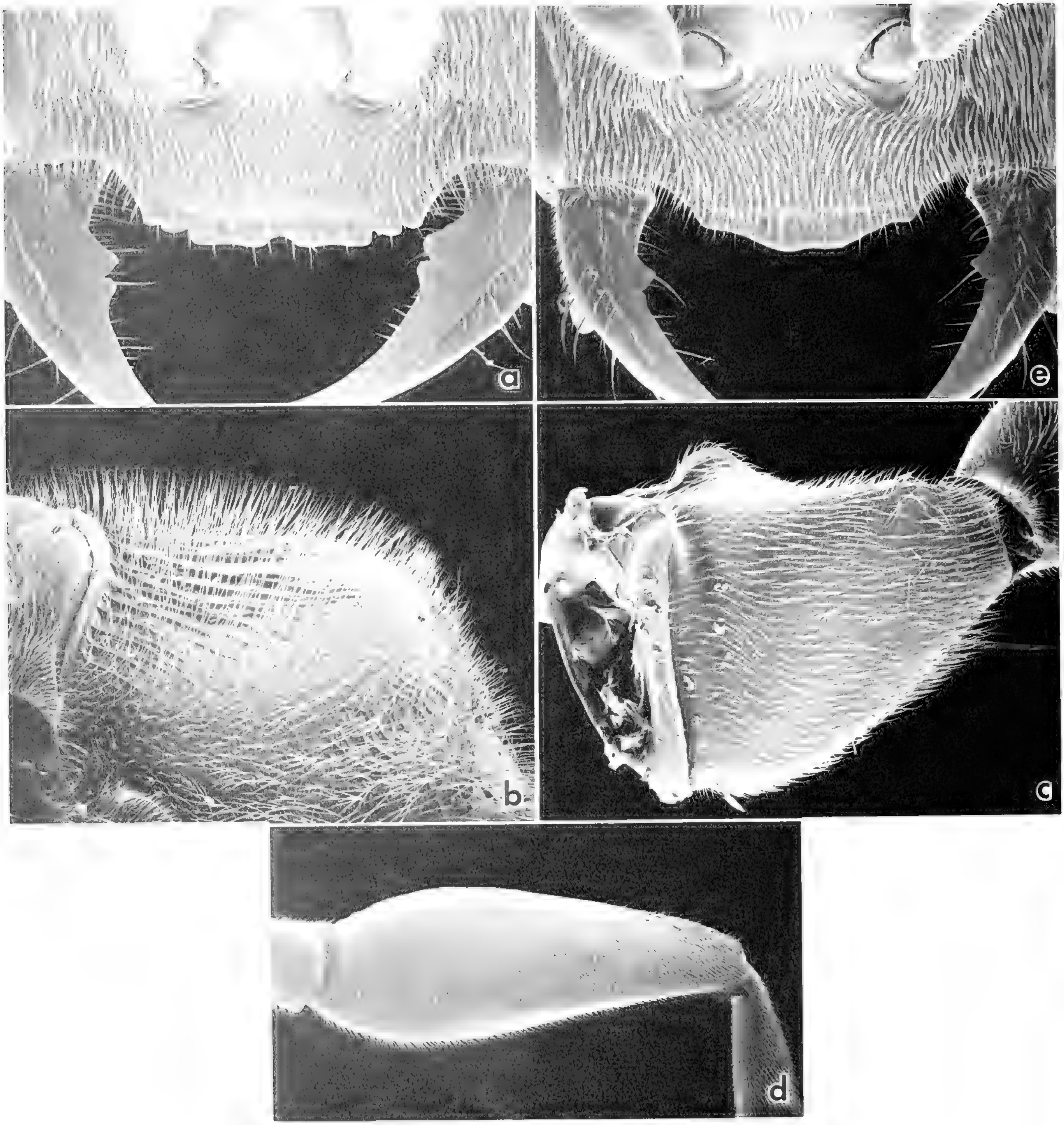

FIGURE 141. *Tachysphex inconspicuus* (Kirby). a—female clypeus, b—female propodeum; c—female hindcoxa; d—female hindfemur; e—male clypeus.

of the genus *Chorisoneura* and *Riatia*. The mutillid *Timulla eriphyla* Mickel is a parasite.

GEOGRAPHIC DISTRIBUTION (Fig. 143).—Central and South America between Tropic of Cancer and Tropic of Capricorn, and also Jamaica (where it occurs sympatrically with *alayoi*, although not in the same habitats).

MATERIAL EXAMINED.—44♀, 55♂ from Mexico and Central America (AMNH, CAS, CIS, CNC, KU, LACM, MCZ, UCD, USU), 5♀, 2♂ from Trinidad and Tobago (FSCA), 3♀, 2♂ from Jamaica (CAS, FSCA).

RECORDS.—MEXICO: **Chiapas:** Ixtapa, 2 mi SE Ococingo, Ocozocoautla, 32 mi W San Cristóbal, Simojovel. **Jalisco:** Barra de Navidad, Chamela, Puerto Vallarta. **Morelos:** 5 mi E Cuernavaca, 6 mi S Temixco. **San Luis Potosí:** El Bonito (7 mi S Ciudad Valles). **Sinaloa:** 3 mi N Elota. **Tamaulipas:** La Pesca, Playa

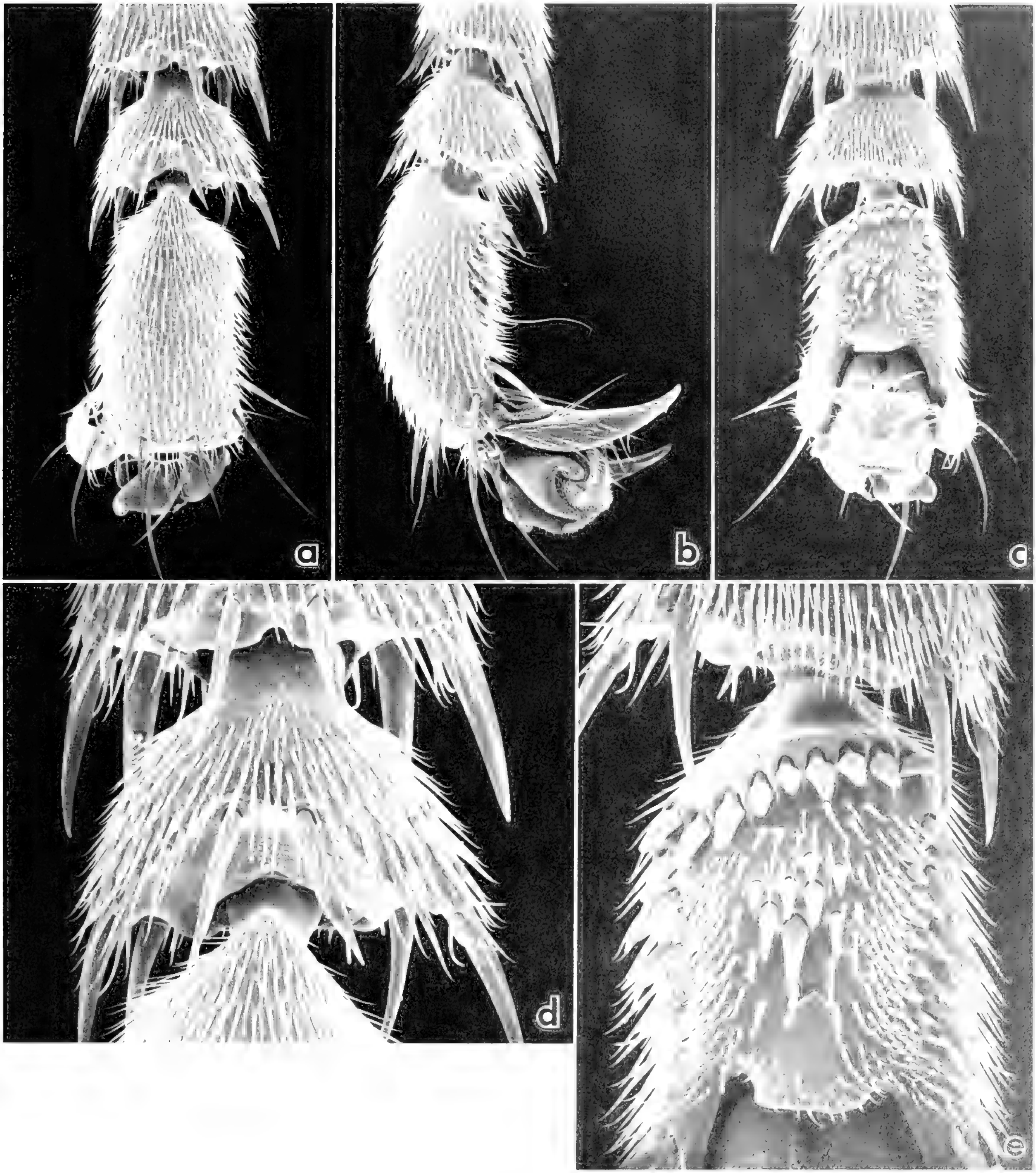

FIGURE 142. *Tachysphex inconspicuus* (Kirby), female: a—apical hindtarsomeres, dorsal view, b—same, lateral view, c—same, ventral view, d—hindtarsomer IV, dorsal view; e—hindtarsomere V, ventral view.

FIGURE 143 Geographic distribution of *Tachysphex inconspicuus* (Kirby).

Altamira Municipio de Aldama (Rancho Nuevo) **Veracruz:** 30 mi S Acayucán, Atovac (Pulawski 1974*a*)

CENTRAL AMERICA. COSTA RICA: Boca de Barranca, La Selva (4 km SE Puerto Viejo) Limón, Tilarán (Pulawski 1974*a*), Tortuguero, Turrialba. GUATEMALA Antigua, Guatalon. PANAMA: Canal Zone and neighboring area (Pulawski 1974*a*), 20 km N Curundú

WEST INDIES JAMAICA: **Portland Parish:** Paradise. **St. Andrew Parish:** Mammee River Valley near Kingston. TRINIDAD AND TOBAGO. **Trinidad:** Simla Field Station **Tobago:** 1 mi ESE Adelphi

SOUTH AMERICA (localities listed in Pulawski 1974*a*, are not repeated here) ARGENTINA **Corrientes:** Puerto Valle–Ituzaingo. COLOMBIA. **Meta:** Carimagua (17 km E El Porvenir). El Porvenir **Valle:** Atuncela. ECUADOR. **Napo:** Limoncocha on Río Napo. PARAGUAY: San Pedro Cororo–Río Ipane. PERU: **Huanuco:** Tingo María in Monson Valley. VENEZUELA: **Aragua:** 16 km NW of Maracay **Guarico:** 44 km S Calabozo

Tachysphex iridipennis (F. Smith)

(Figures 144, 145)

Tachytes iridipennis F. Smith, 1873:57, ♀. ! Holotype: ♀, Brazil: Ega [=Tefé] (BMNH) —In *Tachysphex* Pulawski 1974*a*:80 (full bibliography); Bohart and Menke 1976:274

DIAGNOSIS.—Unlike the other two New World blattid collectors, *iridipennis* lacks the hindcoxal tooth. It differs from *inconspicuus* by the following: in the female, the vertex is broader (width : length = 1.8–2.1 instead of 1.1–1.4), the clypeal lip is not incised laterally (Fig. 144a) (incised in most *inconspicuus*), the hindfemur is stout (Fig. 144b), the apicoventral margin of tarsomere IV is expanded into a lobe, and the pygidial plate of

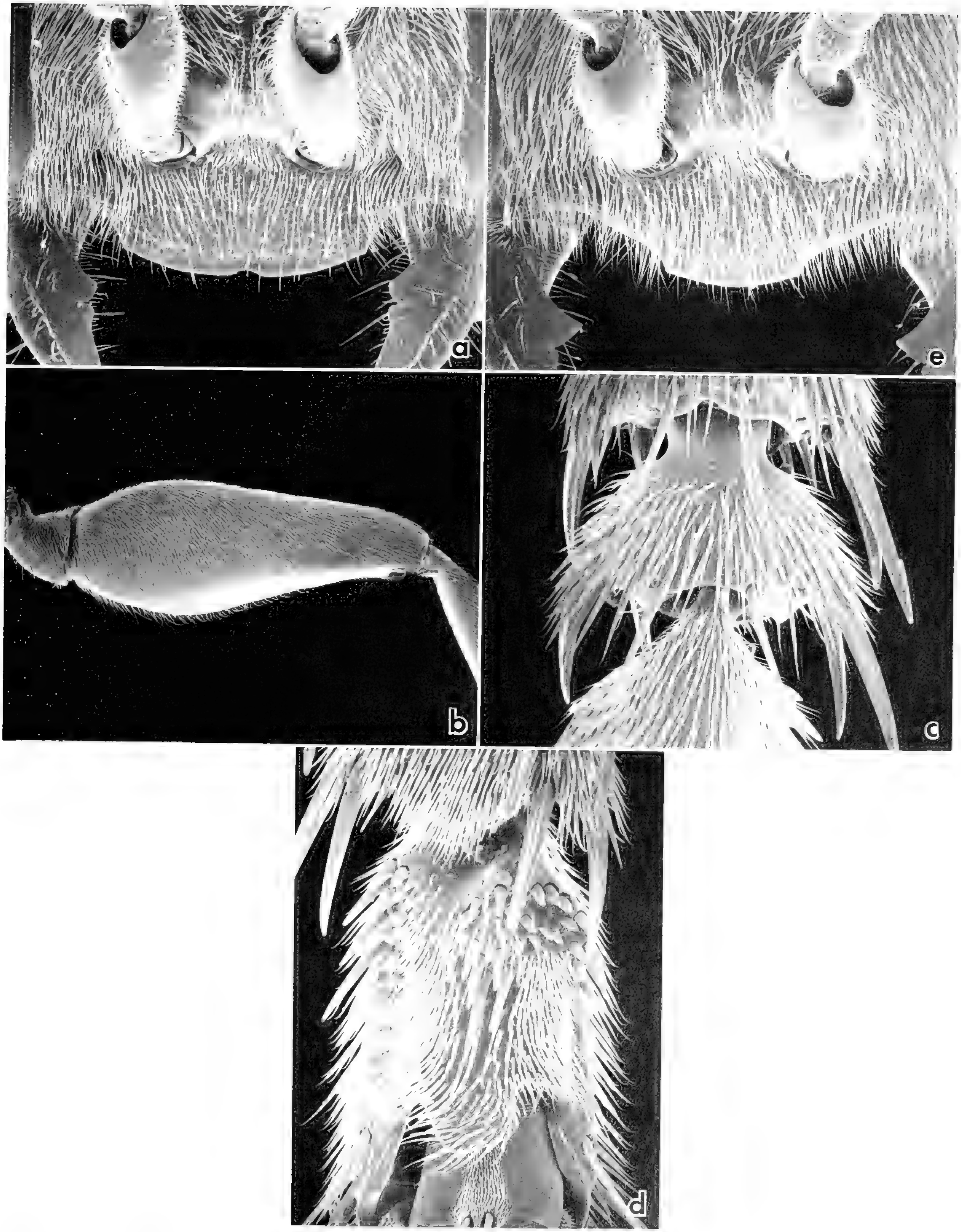

FIGURE 144. *Tachysphex iridipennis* (F. Smith): a—female clypeus; b—female hindfemur, c—female hindtarsomere IV, dorsal view, d—female hindtarsomere V ventral view; e—male clypeus.

many specimens is setose; in the male, sterna III–VI are sparsely punctate and pubescent, and the forebasitarsus has preapical rake spines. The clypeal lobe of the male is narrower (Fig. 144e) than in *alayoi* and most *inconspicuus* (corners closer to each other than to orbit). Unlike *alayoi*, setae of propodeal dorsum are uniformly inclined posterad in *iridipennis* (basomedian setae oriented anterad in *alayoi*), the gaster is all black (gastral tip red in most *alayoi*), and tergum V of most females is densely punctate before the apical depression.

Description.—Scutum longitudinally crenulate along hindmargin. Axilla not steplike. Metapleuron without longitudinal carina beneath flange, the latter moderately broad. Propodeal dorsum longitudinally ridged, carinate along hind and lateral margins; side ridged, but ridges evanescent in occasional specimens. Hindcoxa without basal tooth.

Setae of propodeal dorsum inclined posterad.

Body black, tarsi brown reddish in male (basitarsus in some specimens dark) and occasional females. Terga I–IV (I–III in some males) silvery fasciate apically. Wings hyaline to infumate (slightly so in male).

♀.—Clypeus (Fig. 144a): middle area shiny apically, dull, densely punctate basally (basomedian area, bevel and lip not differentiated); free margin of lobe arcuate or biarcuate, shallowly notched mesally, not incised laterally. Dorsal length of flagellomere I 1.9–2.4× apical width. Vertex width 1.8–2.1× length. Punctures more than one diameter apart on frons (rarely one diameter apart), vertex, scutum, mesopleuron, and mesosternum; fine to coarse on frons (interspaces microsculptured); in most specimens about one diameter apart on tergum V (apical depression impunctate). Mesothoracic interspaces slightly microsculptured, shiny. Pygidial plate in most specimens with elongate punctures and appressed setae that are sparse anteriorly and dense apically, in some specimens with appressed inconspicuous setae. Rake spines of forebasitarsus 1.2–1.7× basitarsal width (2.0× in some Guyanese individuals). Hindfemur stouter than in *inconspicuus* and *alayoi*. Tarsomere IV (Fig. 144c): apical emargination very obtuse, apicoventral margin produced into a lobe. Tarsomere V: Figure 144d. Length 8.0–10.5 mm.

Setae erect, two to three MOD long on vertex; erect or suberect, 1.0–1.7 MOD long on scutum; about 1.5 MOD long on midfemoral venter. Outer face of foretibia sparsely pruinose.

♂.—Clypeus (Fig. 144e): lobe densely punctate, with short, minute carina extending from each lip corner; lip slightly arcuate, indistinctly delimited basally; its corners rounded to sharply prominent, closer to each other than to orbit. Dorsal length of flagellomere I 1.5–2.0× apical width. Frons below midocellus dull or shiny. Vertex width 1.75–2.4× length. Punctures no less than one diameter apart on frons; one to several diameters apart on vertex; coarse on scutum (more than one diameter apart on disk); on mesopleuron coarse except posteriorly, more than one diameter apart (at least posteriorly); in most individuals more than one diameter apart on mesothoracic venter. Tergum VII with sharp, longitudinal carina on side; sterna III–VI pubescent, sparsely punctate. Forefemoral notch deeper than in *inconspicuus* and *alayoi*, with glabrous, sharply delimited bottom. Forebasitarsus with three or four preapical rake spines whose length is less than basitarsus width; apical spine of foretarsomere II much shorter than tarsomere III. Length 5–10 mm.

Setae erect, 2.0–2.5 MOD long on vertex; suberect, 2.0 MOD long on scutum; about 1.5 MOD long on midfemoral venter; suberect, 1.0 MOD long on hindfemoral venter.

Life History.—This species is known to prey upon adults of the roach *Cariblatta tobagensis* Hebard (see Pulawski 1974*a*). In addition, a specimen from El Coco, Costa Rica (CSDA) is pinned with a nearly adult blatellid *Ischnoptera rufa debilis* Hebard (det. D. A. Nickle), and I collected a female carrying an adult blatellid *Euthlastoblatta abortiva* Caudell (det. D. A. Nickle) in Bentsen Rio Grande Valley State Park, Texas.

Geographic Distribution (Fig. 145).—Southern Texas to Tropic of Capricorn.

Material Examined.—9♀, 10♂ from United States, Mexico, and Central America (CAS, CIS, CSDA, FSCA, KU, MCZ, UCD, UCR).

Records (South American localities listed in Pulawski (1974*a*) are not repeated here).—UNITED STATES: TEXAS: **Hidalgo:** Bentsen Rio Grande Valley State Park (2♀, 1♂, CAS)

MEXICO: **Colima:** Manzanillo (Pulawski 1974*a*). **Sinaloa:** 2.5 mi N Mazatlán, Rio Fuerte 11.6 mi N Los Mochis. **Sonora:** Cócorit. **Tamaulipas:** La Pesca, Municipio de Aldama (Pueblo Nuevo), Playa Altamira. **Veracruz:** Minatitlán.

CENTRAL AMERICA: COSTA RICA: **Guanacaste Prov.:** El Coco. PANAMA: Archipelago de las Perlas, Canal Zone and adjacent area (Pulawski 1974*a*).

SOUTH AMERICA: COLOMBIA: **Meta:** El Porvenir. VENEZUELA: **Aragua:** 2 km N Ocumare. **Falcón:** Peninsula Paraguana (Pueblo Nuevo). **Mérida:** 38 km SW Mérida. **Zulia:** Carrasquero, 31 km SW Machiques, Río Palmar 15 km NE Rosario.

Tachysphex alayoi Pulawski

(Figures 145, 146)

Tachysphex alayoi Pulawski, 1974*a*:84, ♀, ♂. ! Holotype: ♀, Cuba: Oriente Province: Juraguya near Guantanamo (USNM).—Bohart and Menke 1976:272; Krombein 1979:1632; Elliott et al. 1979:356.

Diagnosis.—*Tachysphex alayoi* is the only blattid-hunting *Tachysphex* known from Florida and most of the West Indies (but it coexists with *inconspicuus* in Jamaica). Unlike *inconspicuus* and *iridipennis*, basomedian setae of the propodeal dorsum are inclined anterad, and the gastral tip is red in most specimens. Unlike *inconspicuus*, the propodeal side is ridged, the female clypeal lip (Fig. 146a) is not incised laterally (incised in vast majority of *inconspicuus*), the tarsomere IV is very obtusely emarginate, with apicoventral margin produced into a lobe (Fig. 146b, c), and male sterna IV–VI are nearly impunctate and glabrous. Unlike *iridipennis*, the hindcoxa of *alayoi* has a basal tooth, female tergum V is sparsely punctate, and the male clypeal lobe is broad (Fig. 146d), with corners closer to orbit than to each other.

Description.—Scutum not crenulate before hindmargin (but with contiguous punctures). Axilla not steplike. Metapleuron without longitudinal carina beneath flange, the latter narrow. Propodeal dorsum longitudinally ridged (ridges in some individuals inconspicuous or replaced by irregular reticulation), weakly carinate along hindmargin and not carinate along lateral margin; side ridged. Hindcoxa with basal tooth (that is inconspicuous in small males).

Setae erect on vertex and scutum, on propodeal dorsum inclined anterad basomedially and posterad laterally and posteriorly.

Terga I–IV (I–III in many females) silvery fasciate apically. Wings hyaline.

♀.—Clypeus (Fig. 146a): middle section with large punctures, microsculptured along frontoclypeal suture; lip absent or indistinct; free margin of lobe sinuate, emarginate mesally, not in-

FIGURE 145. Geographic distribution of *Tachysphex alayoi* Pulawski and *iridipennis* (F. Smith)

cised laterally. Dorsal length of flagellomere I 1.8–2.3× apical width. Vertex width 1.3–1.6× length. Punctures about one diameter apart before midocellus (interspaces microsculptured); large, at least one diameter apart behind postocellar impression; more than one diameter apart on mesopleuron and mesothoracic venter, fine on mesopleuron (interspaces alutaceous); many diameters apart on tergum V. Some punctures of scutal disk subcontiguous, others slightly more than one diameter apart. Pygidial plate fairly broad (also apically), asetose. Rake spines of forebasitarsus 1.4–1.6× width of basitarsus. Hindfemur stout, as in *iridipennis*. Tarsomere IV (Fig. 146b, c): apical emargination IV very obtuse; apicoventral margin produced into a lobe. Tarsomere V: Figure 146c. Length 6–12 mm.

Setae length (in MOD): 2.0 or nearly so on vertex, 1.5–1.7 on scutum, 1.5 on midfemoral venter. Outer face of foretibia glabrous.

Gastral segments IV–VI red or more or less darkened. Legs black, inner face of foretibia brownish.

♂.—Clypeus (Fig. 146d): middle section closely punctate (in some specimens punctures sparse anteriorly); lip absent or inconspicuous; lateral corners of lobe distinct (prominent in some specimens), closer to orbits than to each other. Dorsal length of

flagellomere I 1.5–1.9× apical width. Vertex width 1.6–1.8× length. Punctures shallow on frons, averaging less than one diameter apart (interspaces coarsely microsculptured); less than one to more than one diameter apart behind postocellar impression; less than one diameter apart on scutum; subcontiguous on mesopleuron anteriorly, more than one diameter apart posteriorly; no less than one diameter apart on mesothoracic venter. Apical depression of sterna II and III impunctate, glabrous, sterna IV–VI nearly so. Forefemoral notch glabrous. Foretarsal rake absent or rudimentary (rake spines of forebasitarsus equal to width of basitarsus or slightly longer); outer apical spine of foretarsomere II much shorter than tarsomere III. Length 5.5–8.5 mm.

Setae length (in MOD) 1.5–1.8 on vertex, 1.2–1.4 on scutum, about one on midfemoral venter, one on basal half of hindfemoral venter.

Gastral segments V–VII, or (some specimens) gaster all black. Legs black or (some individuals) tibiae partly and tarsi reddish.

VARIATION.—In West Indian females, the middle clypeal section may be smooth or microsculptured along the frontoclypeal suture, and the vertex and mesopleural punctation can be coarse or fine. In West Indian males, the glabrous area of the forefemoral notch may be small or large. See Pulawski (1974*a*) for details.

LIFE HISTORY.—Pulawski (1974*a*) noted an undetermined blattid nymph as prey of this species. Elliott et al. (1979) reported adults and nymphs of the roach *Symploce* sp. near *munda* Gurney as prey.

GEOGRAPHIC DISTRIBUTION (Fig. 145).—Southern Florida and Caribbean Islands (Bahama Islands, Cuba, Dominican Republic, Jamaica, Puerto Rico, Virgin Islands).

RECORDS AND MATERIAL EXAMINED (localities listed in Pulawski (1974*a*) are not repeated here).—UNITED STATES: FLORIDA: **Broward:** Dania, coast pine forest (6♀, 26♂; BMNH, USNM, WJP).

BAHAMA ISLANDS: **Eleuthera Island:** Rainbow Bay (1♀, 1♂, FSCA). **Great Sale Cay** (1♂, AMNH). **San Salvador** (Elliott et al. 1979).

DOMINICAN REPUBLIC (10♀, 71♂, CAS, FSCA, UCD): **Barahona:** Barahona (also 7 km E), Paraiso. **Distrito Nacional:** Haina, Santo Domingo (Jardín Botánico). **La Altagracia:** Boca de Yuma, Playa del Muerto E Nisibón. **Pedernales:** Cabo Rojo, Oviedo. **Puerto Plata:** Playa Cabarete (32 km E Puerto Plata). **Samana:** Honduras

JAMAICA (9♀, 13♂; CAS, FSCA, IJ): **Hanover Parish:** Paradise. **Kingston Parish:** The Palisadoes. **Manchester Parish:** beach 15 km E Alligator Ponds. **St. Catherine Parish:** Port Henderson (also 7.5 air km SW). **St. Thomas Parish:** Mammee Bay, Yallahs

julliani Species Group

Species of the *julliani* group have a truncate propodeum (hindface almost vertical), the apical sterna of males are glabrous (sparsely pruinose in some *coquilletti*), and the foretarsomeres are not expanded. In females of most species, the apical gastral segments have thickened preapical bristles (Fig. 147c, d), and the pygidial plate is either unusually broad (Fig. 147e) or has a distinctive sculpture. Members of the *albocinctus* group (which is not found in North and Central America) are similar, but their foretarsomeres I and II are expanded. I previously (Pulawski 1971) separated the *albocinctus* and *julliani* groups by the shape of the hindwing jugal lobe and inclination of crossvein cu-a, but subsequently (Pulawski 1977*a*) found that these features are intermediate in some Australian species. In other groups, the prepodeum is either truncate or inclined and the male sterna are setose or fasciate, but glabrous in some species.

Species of the *julliani* group provision with mantids. The group occurs in the Palearctic, Afrotropical, Nearctic, and northern part of the Neotropical Region. Only two species are known in the New World: *cockerellae* and *coquilletti*.

Characters shared by *cockerellae* and *coquilletti* are: article V of maxillary palpus as long as IV; frons, scutum, and mesothoracic venter with well-defined, nearly contiguous punctures; mesopleuron and in some specimens scutum punctatorugose; propodeal dorsum microreticulate to irregularly rugose. Vestiture of gena, thorax, and femora not obscuring sculpture, but frontal integument hidden between antennal socket and orbit; setae appressed on scutum and mesothoracic venter; propodeal dorsum with setae directed posterad on lateral zone, directed anterad on mesal, triangular zone. Female: preapical setae of gastral segments thickened (especially on sterna IV and V); tergum V with a few, scattered punctures; pygidial plate (Fig. 147e) very broad, broadly rounded apically, smooth; venter of tarsomeres V with two or three spines (one basal, one apical); setae 1.0 MOD long on midfemoral venter; gaster red. Male: middle clypeal lobe almost flat; corners obtuse to rectangular, projecting over clypeal free margin (except in many *coquilletti*); distance between corner and orbit twice distance between corners; terga V and VI with impunctate apical depressions; punctures of tergum VII sparse basally, dense apically; sterna III–VI glabrous, impunctate or sparsely punctate (but sternum III or III and IV densely punctate laterally); forecoxa densely punctate; forefemoral notch deep, sharply delimited anteriorly and posteriorly; foretarsal rake present, apical spine of foretarsomere II slightly shorter to longer than foretarsomere III. Both *coquilletti* and *cockerellae* resemble the Old World species *julliani*, in which, however, the female pygidial plate has a transverse furrow, and the male clypeus and genitalia are different.

Among the New World species, females can be easily recognized as belonging to the *julliani* group by the broad pygidial plate (Fig. 147e) and thick gastral bristles (Fig. 147c, d). Males can be recognized by the following combination of characters: clypeal lobe narrow (Fig. 148a, b); vertex longer than wide; terga V and VI with glabrous, apical depressions; sterna III–VI impunctate or sparsely punctate, glabrous at least mesally; and the forefemoral notch sharply margined anteriorly and posteriorly (Fig. 148c, d; 150c), its surface is slightly raised above adjacent area. Some of these characters occur in many species belonging to other groups (e.g., the narrow vertex), and some are found in only a few other species. Similar terga and sterna are found in *menkei* and in *mirandus*, and the forefemoral notch is margined in some *iridipennis* and some *powelli*.

Tachysphex coquilletti Rohwer

(Figures 147–149)

Tachysphex coquilletti Rohwer, 1911:572, ♀, ♂. ! Holotype: ♀, California: Los Angeles Co.: no specific locality (USNM).—G. Bohart 1951:950; Krombein 1961:81, Kurczewski 1966*a*:317; Krombein 1967:393; Alcock and Gamboa 1975:164; Hurd and Linsley 1975:116; Bohart and Menke 1976:273; Krombein 1979.1632

Tachysphex dentatus Williams, 1914:169, ♀. ! Holotype: ♀, Kansas: Morton Co.: no specific locality (KU). Synonymized by G. Bohart 1951:950.—LaBerge 1956: 527, Arnaud 1970:332.

DIAGNOSIS.—*Tachysphex coquilletti* differs from *cockerellae*, its closest relative, in having appressed or nearly appressed vertex setae and the propodeal side unridged or weakly ridged. In

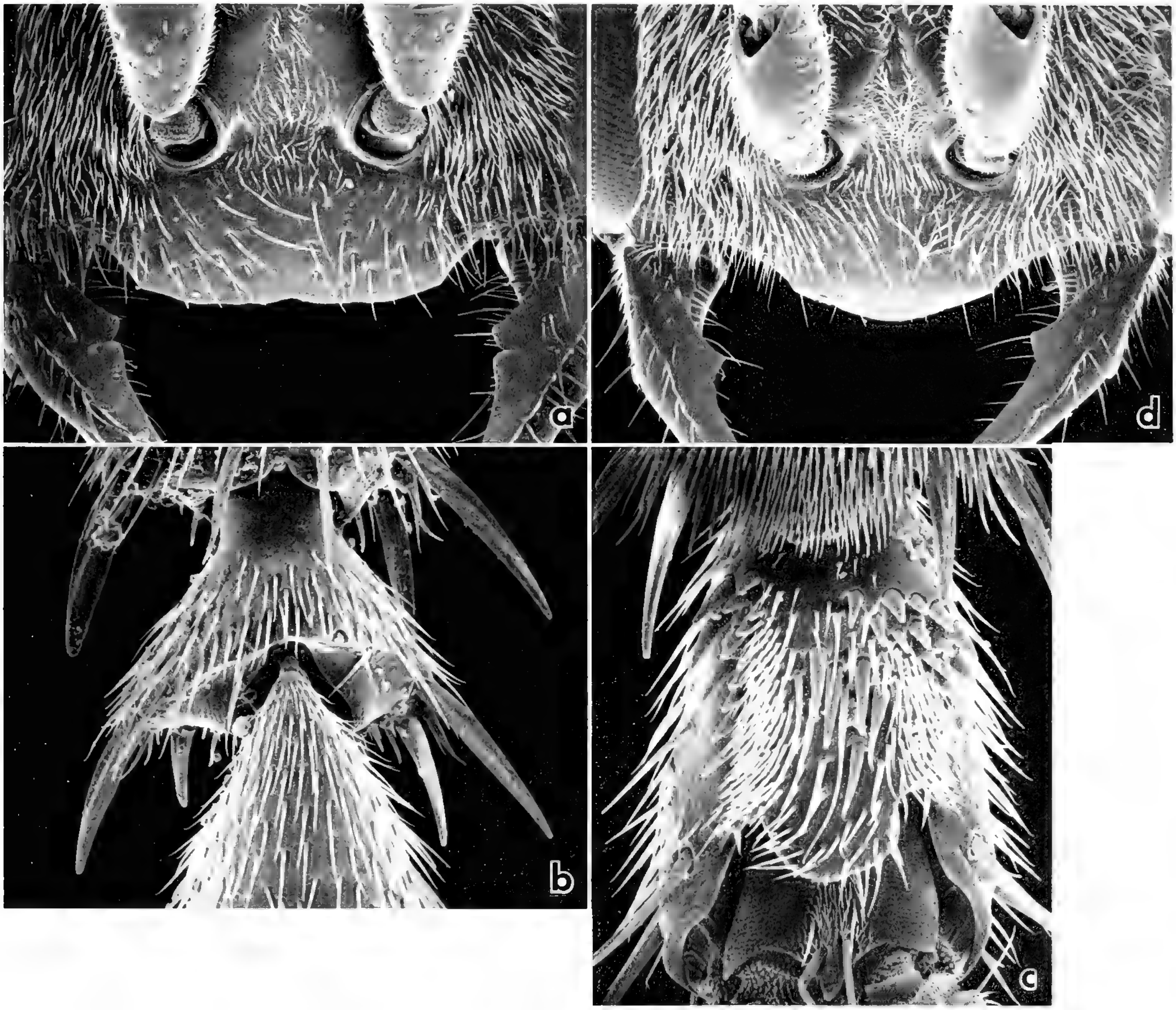

FIGURE 146. *Tachysphex alayoi* Pulawski: a—female clypeus; b—female hindtarsomere IV; c—female hindtarsomere V, ventral view; d—male clypeus.

the female, the clypeal lip is roundly swollen throughout (Fig. 147a, b); in the male, the gaster is dark apically, and the volsella is distinctive (Fig. 148f).

DESCRIPTION.—Vertex longer than wide or (some specimens) as long as wide. Propodeal side microareolate or finely ridged (only posteriorly so in male).

Vertex setae appressed or subappressed.

Head and thorax black, gastral segments I–IV (I–III in many females) silvery fasciate apically. Wings hyaline.

♀.—Clypeus (Fig. 147a, b): bevel shorter than basomedian area, roundly swollen throughout; lip with up to five obtuse teeth, but only median tooth distinct in some individuals. Vertex punctures less than one diameter apart. Length 6.5–9.5 mm.

Setae length 1.0 MOD on vertex, 1.5 MOD on lower gena.

Gaster red. Legs black, tarsi reddish; hindfemur and hindtibia red in some specimens, occasionally also part of midtibia.

♂.—Clypeus (Fig. 148a, b): bevel much shorter than basomedian area; lip with or without median tooth. Vertex indistinctly punctate, punctures less than one diameter apart. Forefemoral notch finely unevenly microrugose (Fig. 148c, e). Length 5–8 mm. Volsella: Figure 148f.

Setae length about 0.6 MOD on vertex, 1.0 MOD on lower gena.

Gastral segments I–III red, remainder brown. Legs black.

LIFE HISTORY.—Many specimens were collected on flowers of *Atriplex semibaccata* R. Br. by F. X. Williams at Chula Vista, California. Alcock and Gamboa (1975) observed a female performing an orientation flight, flying off, and coming back to the nest with an immature mantid, *Litaneutria minor* (Scudder). The nest was 12 cm long. The burrow ran in an arc just below the surface for the first 8 cm, and then it dropped sharply down to a cell 4 cm below the surface. The only previous prey record

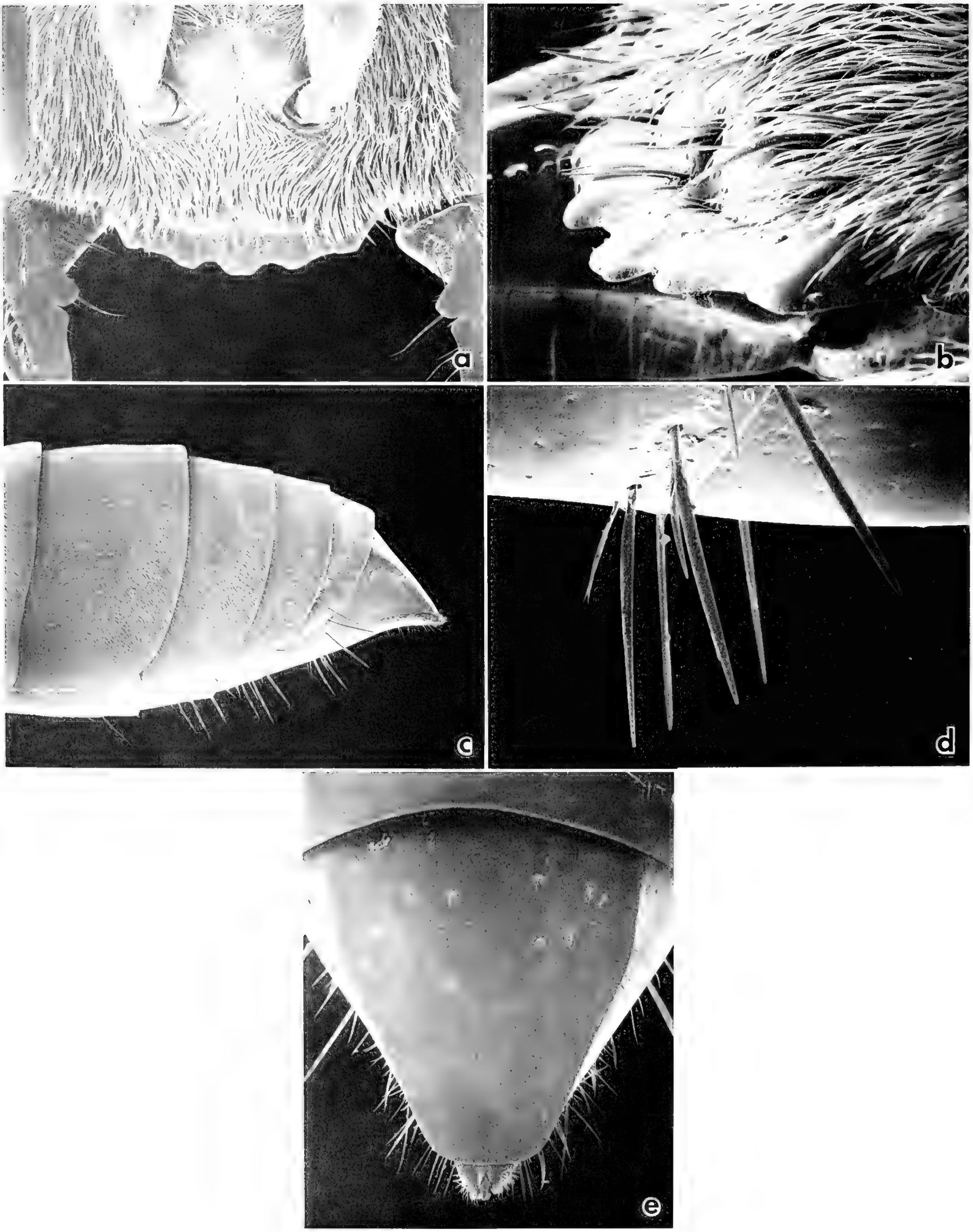

FIGURE [illegible]. *Tachysphex coquilletti* (Rohwer), female: a—clypeus, front view, b—clypeus obliquely from the side, c—gaster, d—sternal setae; e—pygidial plate

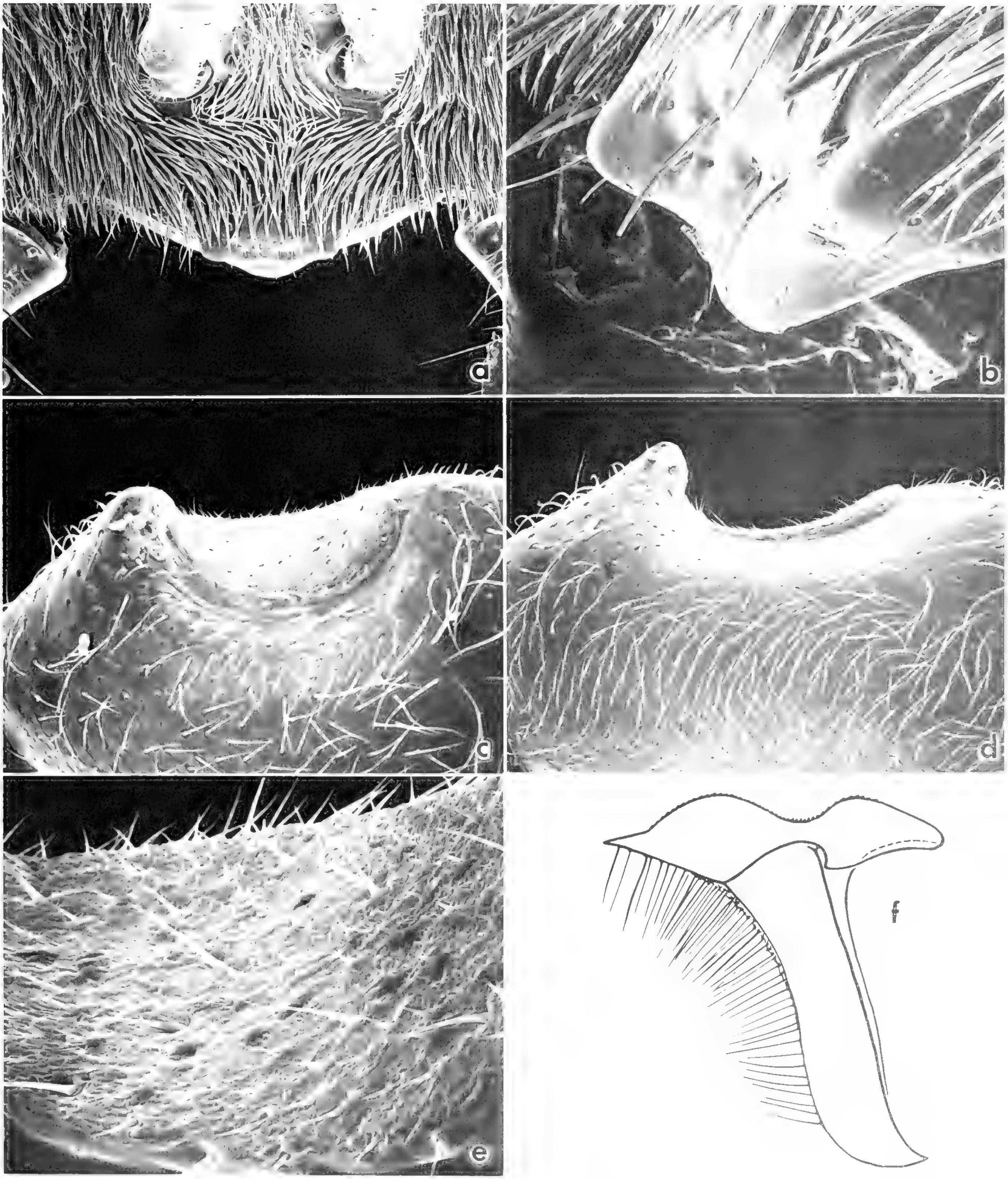

FIGURE 148. *Tachysphex coquilletti* Rohwer, male: a—male clypeus, b—clypeal lobe obliquely from the side, c—forefemoral notch, d—same in a different position, e—bottom of forefemoral notch; f—volsella

FIGURE 149. Geographic distribution of *Tachysphex coquilletti* Rohwer

(G. Bohart 1951, as *tarsatus*, corrected by Kurczewski 1966*a*) was also a *Litaneutria*.

GEOGRAPHIC DISTRIBUTION (Fig. 149).—North America west of 95th meridian north to Kansas, Idaho, and Oregon; south to Tropic of Cancer.

MATERIAL EXAMINED.—665♀, 658♂.

RECORDS.—UNITED STATES: ARIZONA: **Cochise. Coconino:** 20 mi N Flagstaff, The Gap. **Gila:** Cedar Creek (15 mi W Fort Apache), 3 mi SE Christmas. **Graham:** 6 mi S Safford (also 16 mi E). **Maricopa. Mohave. Pima. Pinal. Santa Cruz:** Patagonia, Santa Rita Mts. **Yavapai:** 20 mi NW Wickenburg. **Yuma.** CALIFORNIA: **Alameda:** 10 mi E Livermore, Tesla Road. **Contra Costa:** Antioch. **Fresno. Imperial. Inyo. Kern. Kings:** Avenal, Lemoore. **Lassen:** Hallelujah Junction, Hot Spring Mt. **Los Angeles. Marin:** Ross. **Merced:** Dos Palos. **Mono:** 11 mi N Bridgeport. **Monterey:** 10 mi N Parkfield. **Orange:** Anaheim, Irvine Park, Potrero Canyon. **Plumas:** Beckwourt Summit. **Riverside. San Benito:** Clear Creek Recreation Area, Panoche. **San Bernardino. San Diego. San Luis Obispo:** 5 mi S Creston. **Santa Barbara:** Bluff Camp (San Rafael Mts.). **Sierra:** Sierraville. **Stanislaus:** Patterson. **Tulare:** Goshen Junction, Woodlake. **Ventura:** Hungry Valley (5 mi S Gorman), Lockwood Valley, Quatal Canyon (NW corner of county). **Yolo:** Davis, Woodland. COLORADO: **Bent:** 2 mi S Hasty. **Boulder:** Boulder. **Weld:** Crow Valley grassland area, Owl Creek (12 mi NE Nunn). IDAHO: **Cassia:** 4 mi SE Malta. **Owynza:** Murphy. **Oneida:** Curlew Reservoir. KANSAS: **Morton:** —. **Wallace:** Sharon Springs. NEVADA: **Churchill:** Fallon. **Clark:** Juanita Spring Ranch (10 mi S Riverside), Moapa, 10 mi S Searchlight. **Eureka:** 6 mi S Beowawe, 14 mi W Eureka. **Lincoln:** Tule Desert (E Carp). **Mineral:** 8 mi S Mina, 10 mi W Montgomery Pass, 4.5 mi S Schurz. **Nye:** Mercury, 13 mi W Warm Springs. **Pershing:** Lovelock (also 8 mi S). **Washoe:** Hwy. 81 (54 mi NW Gerlach), Pyramid Lake (S shore), Reno. **White Pine:** Charcoal Oven State Park, Connor Pass. NEW MEXICO: **Bernalillo:** Albuquerque. **Catron:** Pie Town. **De Baca:** Sumner Lake State Park. **Dona Ana:** Hatch, Las Cruces, Mesilla Park. **Eddy:** 15 mi E Hope. **Hidalgo. Lincoln:** Carizzozo. **Luna:** Columbus. **Otero:** Alamo Canyon near Alamogordo. **Quay:** Tucumcari. **Roosevelt:** Portales. **Torrance:** Estancia, Moriarty, Gran Quivara (town). OKLAHOMA: **Marshall:** Lake Texoma (2 mi E Willis). OREGON: **Deschutes:** Smith Rock State Park. TEXAS: **Brewster:** Alpine, Big Bend National Park (Boquillas, Grapevine Spring, Nine Point Draw, Panther Junction, Santa Elena Canyon), 34 mi S Marathon. **Cameron:** Port Isabel. **Guadalupe:** Seguin. **Hidalgo:** McAllen Botanical Garden. **Hudspeth:** McNary, 5 mi E Sierra Blanca. **Jeff Davis:** 23 mi W Fort Davis, Valentine. **Mitchell:** Lake Colorado City State Park. **Presidio:** Presidio. **Starr:** Rio Grande City. **Ward:** 1 mi S Grandfalls. UTAH: **Box Elder:** 13 mi W Lakeside, 25 mi SW Snowville. **Emery:** 9 air mi E Castledale, Green River, Wild Horse Creek N Goblin Valley. **Garfield:** Shootaring Canyon. **San Juan:** 6 mi S Hall's Crossing, Kane Springs (E Natural Bridges National Monument). **Uintah:** SW Bonanza. **Washington.**

MEXICO: **Baja California Norte. Baja California Sur. Chihuahua:** 12 mi N Escalón, 10 km S Villa Ahumada. **Coahuila:** 10 km SW Cuatrociénegas. **Durango:** 5 mi W Durango. **Sinaloa:** 8 mi SE Elota. **Sonora:** Alamos (also 10 mi SE), Bahía San Carlos, Cócorit, 19 mi S Estación Llano, Guaymas, 8 mi S Santa Ana, 15 mi E Yavaros. **Zacatecas:** 9 mi N Ojo Caliente.

Tachysphex cockerellae Rohwer

(Figures 150, 151)

Tachysphex cockerellae Rohwer, 1914:518, ♂.! Holotype: ♂, Guatemala: Amatitlán (USNM).—Krombein 1967:393; Pulawski 1974*a*:88; Bohart and Menke 1976: 273; Krombein 1979:1632; Elliott and Kurczewski 1985:296.

DIAGNOSIS.—*Tachysphex cockerellae* differs from its closest relative *coquilletti* in having erect vertex setae and a ridged propodeal side (not ridged in some males). The clypeal bevel of the female is ridgelike, overhanging the lip base laterally (Fig. 150a, d), and the vast majority of males have an all red gaster.

DESCRIPTION.—Propodeal side ridged, but ridges evanescent in occasional males.

Vertex setae erect, 1.0 MOD long.

Head, thorax, and legs black, tarsi reddish or (most males) black. Gaster red in most specimens, but abdomen largely darkened in a male from Wagon Road No. 2 Campground, California

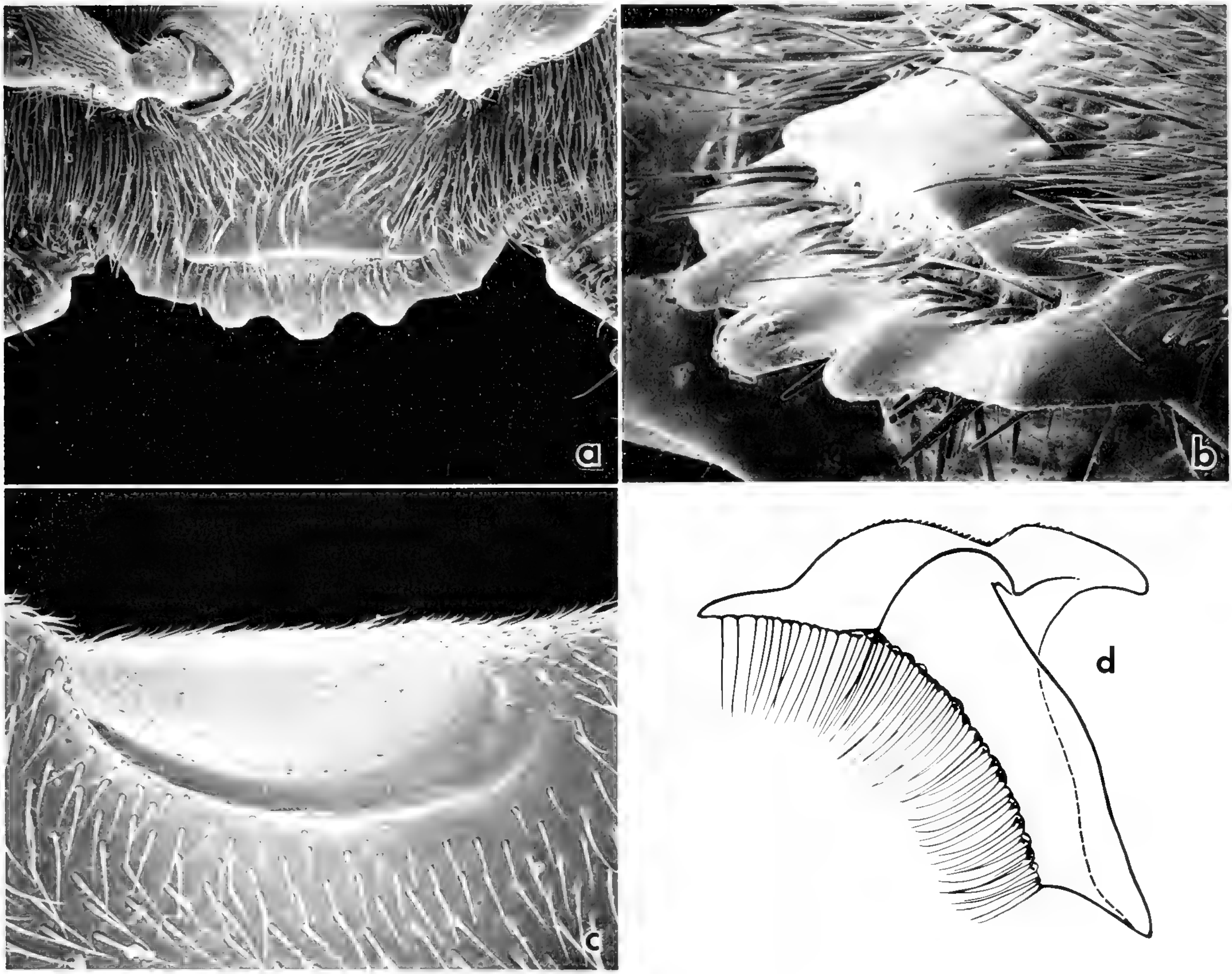

FIGURE 150. *Tachysphex cockerellae* Rohwer: a—clypeus of female; b—clypeus of female obliquely from the side; c—forefemoral notch of male; d—volsella.

(CAS). In this specimen, all sterna are black (except sternum II red laterally), and terga IV–VII are blackish. Terga I–IV (I–V in many males) silvery fasciate apically. Wings hyaline.

♀.—Clypeus (Fig. 150a, b): bevel shorter than basomedian area, ridgelike, especially laterally where it overhangs base of lip; lip with three to five obtuse teeth or (some specimens) only one distinct tooth (median or lateral). Vertex as long as wide or slightly longer, with well-defined punctures that are no more than one diameter apart. Length 8–12 mm.

♂.—Clypeus: bevel much shorter than basomedian area to almost absent; lip usually with median tooth. Vertex longer than wide, its punctures less than one to more than one diameter apart. Forefemoral notch micropunctate (Fig. 150c). Length 7.9–9.8 mm.

LIFE HISTORY.—A female from Napa County, California, is pinned with a nymphal mantid *Litaneutria minor* (Scudder) according to Elliott and Kurczewski (1985).

GEOGRAPHIC DISTRIBUTION (Fig. 151).—Southern Oregon to northern Colombia, eastward to New Mexico and southwestern Texas, also southwestern Utah.

MATERIAL EXAMINED.—448♀, 547♂.

RECORDS.—UNITED STATES: ARIZONA: **Cochise. Gila:** 3 mi SW Christmas. **Graham:** Roper Lake State Park. **Maricopa:** 3.5 mi S Cave Creek, Phoenix, 3 mi SW Wickenburg. **Mohave:** Cattail Cove (9 mi N Parker Dam), Mohave Valley. **Pima. Pinal:** Oracle (also 3 mi SW), 3 mi W Superior. **Santa Cruz. Yavapai:** Prescott. **Yuma:** Parker, Quartzsite, Tinajas Altas. CALIFORNIA: **Alameda:** Tesla Road. **Calaveras:** Mokelumne Hill. **Colusa:** Lagoda, 10 mi SW Stonyford. **Contra Costa:** Mt. Diablo. **Fresno:** 8 mi NW Coalinga. **Imperial. Inyo:** 7 mi N Parcher's Camp (ca. 14 mi W Big Pine). **Kern:** Antelope Canyon near Tehachapi, Mill Potrero, Walker Pass. **Los Angeles. Modoc:** Alturas. **Mono:** 2.5 mi S Bridgeport, 1 mi SW Tom's Place, Topaz Lake. **Napa:** —(August 1898). **Riverside. San Bernardino:** Miller Canyon, Needles. **San Diego:** Borrego Valley, Scissors Crossing, Vallecitos. **Santa Barbara:** Bluff Camp, Figueroa Mts., Santa Ynez Mts. **Santa Clara:** Arroyo Mocho (25 mi S Livermore). **Shasta:** Old Station, 10 mi N Redding. **Sierra:** Sierraville. **Siskiyou:** Klamath River 8 mi N Yreka. **Stanislaus:** Del Puerto Canyon. **Tehama:** Manton. **Tulare:** Ash Mountain (Kaweah Power Station). **Tuol-**

FIGURE 151. Geographic distribution of *Tachysphex cockerellae* Rohwer.

umne: 6 mi E Tuolumne City. **Ventura:** Wagon Road No. 2 Campground (18 air mi WSW Gorman). NEVADA: **Clark:** Charlestown Mts. (Willow Creek Camp), Mt. Springs Summit. **Washoe:** Galena Creek, Mt. Rose. NEW MEXICO: **Luna:** 6 mi NW Florida. **Otero:** Alamogordo, Cloudcroft. **Sierra:** Percha Dam State Park. **Socorro:** Bernardo, La Joya (20 mi N Socorro). OREGON: **Josephine:** Rough and Ready Botanical Wayside 5 mi S Cave Junction (LACM). TEXAS: **Brewster:** Big Bend National Park (Santa Elena Canyon). UTAH: **Washington:** Leeds Canyon, Zion National Park.

MEXICO: **Baja California Norte:** 10 mi S Mexicali. **Baja California Sur:** El Pescadero, Los Barriles, Miraflores (4 mi WSW), 35 km S Mulegé, 10 mi N San Lucas. **Chiapas:** 5 mi E Cintalapa, 18 km S La Trinitaria, Tuxtla Gutiérrez, Villa Flores. **Colima:** Río Salado 7 km S Colima. **Durango:** 5 mi W Durango, 4 mi N Nombre de Díos. **Guerrero:** 8 mi N Chilpancingo, Zihuatenejo. **Jalisco:** Plan de Barrancas, Puerto Vallarta. **Morelos:** 3 mi N Alpuyeca, 5 mi E Cuernavaca, Lake Tequesquitengo. **Nayarit:** 13 mi SW Tepic. **Oaxaca:** 23 mi S Matias Romero, 62 mi W Tehuantepec. **Puebla:** 3 mi NW Petlalcingo (also 3 mi SE). **Querétaro:** 12 mi NW Querétaro. **Sinaloa:** 10 mi W Concordia, 3 and 8 mi N Elota, 54 mi S Culiacán, 14 mi S Los Mochis, Playa Baviri (17 mi W Los Mochis). **Sonora:** La Aduana, Alamos, Bahía San Carlos, Cócorit, Guaymas. **Tamaulipas:** Matamoros, Tampico.

CENTRAL AND SOUTH AMERICA: COSTA RICA: Cordillera de Guanacasta, Junquillal beach, Puntarenas, Río Corbici near Cañas, 4 km W Turrialba. GUATEMALA: Amatitlán. COLOMBIA: **Atlantico Prov.:** Barranquilla. VENEZUELA: **Guarico Prov.:** Rio Orituco 15 km S Calabozo.

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